

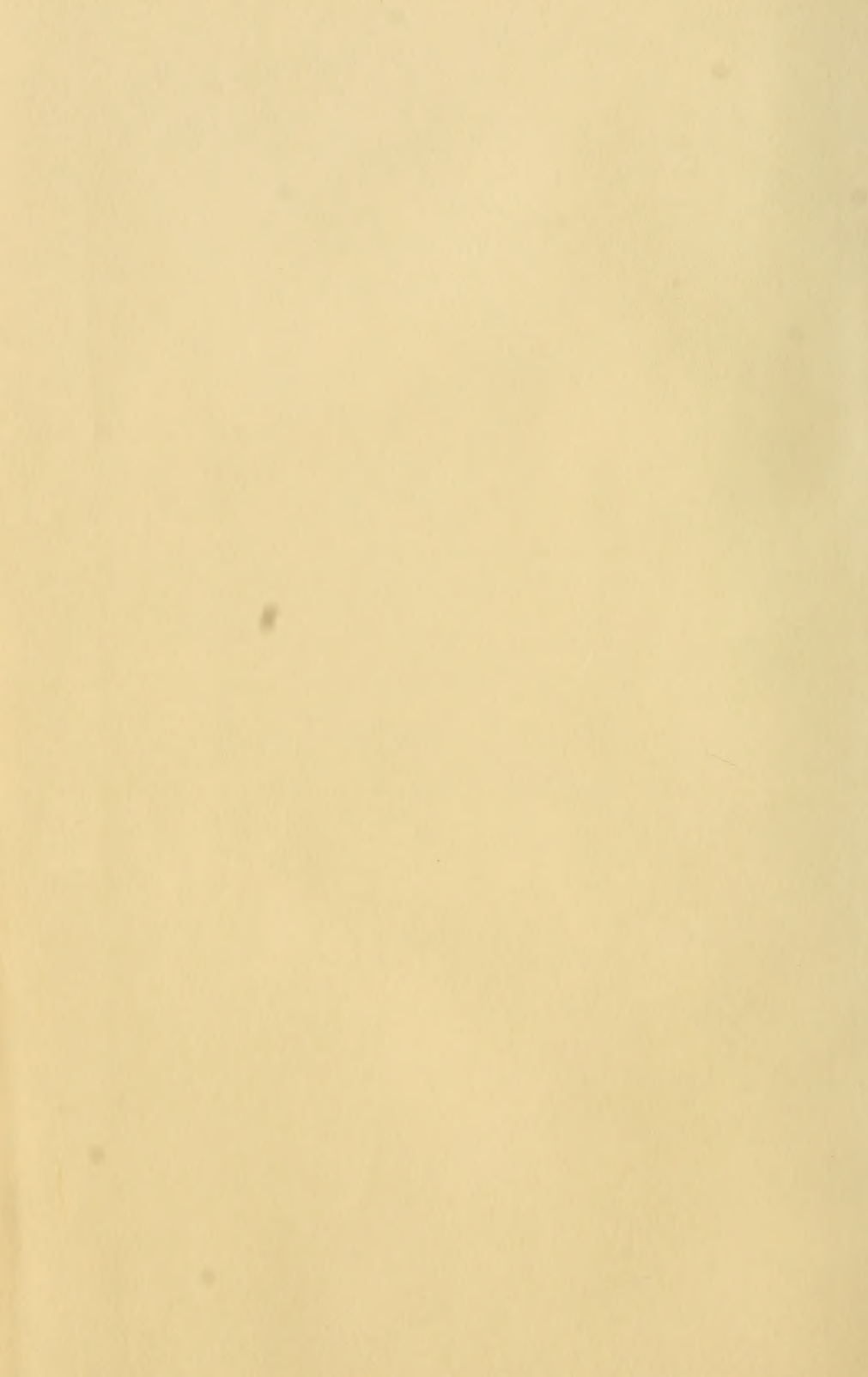
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QUARTERLY JOURNAL

OF

MICROSCOPICAL SCIENCE.

EDITED BY

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OF SCIENCES OF PHILADELPHIA; FOREIGN MEMBER OF THE ROYAL SOCIETY OF
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CONTENTS.

CONTENTS OF No. 185, N.S., MAY, 1903.

MEMOIRS:

	PAGE
The Genera and Species of the Order Symphyla. By H. J. HANSEN (Copenhagen). (With Plates 1—7)	1
On the Body-cavities and Nephridia of the Actinotrocha Larva. By EDWIN S. GOODRICH, M.A., Fellow of Merton College, Oxford. (With Plates 8 and 9)	103
Enteropneusta from Madras. By K. RAMUNNI MENON, Assistant Professor, Presidency College, Madras. (With Plate 10)	123
On Planktonetta atlantica, Borget. By G. HERBERT FOWLER, B.A., Ph.D., F.Z.S. (With Plates 11 and 12)	133

CONTENTS OF No. 186, N.S., JULY, 1903.

MEMOIRS:

On Peripatus guianensis (sp. nov.). By RICHARD EVANS, M.A., D.Sc.(Oxon.), Curator of the Museum, Georgetown, British Guiana. (With Plates 13 and 14)	145
Observations on Ovarian Ova and Follicles in Certain Teleostean and Elasmobranch Fishes. By WILLIAM WALLACE, B.Sc. (With Plates 15—17)	161
A New Koenenia from Texas. By AUGUSTA RUCKER, of the University of Texas, U.S.A. (With Plate 18)	215
Oligotrema psammites: a New Ascidian belonging to the Family Molgulidæ. By GILBERT C. BOURNE, D.Sc., F.L.S., Fellow and Tutor of New College, Oxford; University Lecturer in Comparative Anatomy. (With Plates 19—23)	233

CONTENTS OF No. 187, N.S., DECEMBER, 1903.

MEMOIRS:

	PAGE
On the Anatomy and Development of <i>Distomum cirrigerum</i> , v. Baer. By ERNEST WARREN, D.Sc., Assistant Professor of Zoology, University College, London. (With Plates 24—26) .	273
Studies in the Retina. Part VI.—The Continuity of the Nerves through the Vertebrate Retina. By H. M. BERNARD, M.A. Cantab. (From the Zoological Laboratories of the Royal College of Science.) (With Plates 27—29)	303
The Bionomics of <i>Convoluta roscoffensis</i> , with Special Refer- ence to its Green Cells. By F. W. GAMBLE, D.Sc., Owens College, Manchester; and FREDERICK KEEBLE, M.A., University College, Reading. (With Plates 30 and 31)	363
<i>Trypanosoma</i> in Birds in India. By W. HANNA, M.B., D.P.H., Liverpool. (With Plate 32)	433
On the Modification of the Eye Peduncles in Crabs of the Genus <i>Cymonomus</i> . By E. RAY LANKESTER, M.A., LL.D., F.R.S., Director of the Natural History Departments of the British Museum. (With Plates 33 and 34)	439

CONTENTS OF No. 188, N.S., MARCH, 1904.

MEMOIRS:

On the Dermal Fin-rays of Fishes—Living and Extinct. By EDWIN S. GOODRICH, M.A., Fellow of Merton College, Oxford. (With Plates 35—41)	465
The Structure and Classification of the Arthropoda. By E. RAY LANKESTER, M.A., LL.D., F.R.S., Director of the Natural His- tory Departments of the British Museum. (With Plate 42) .	523
Some Problems of Reproduction.—II. By Professor MARCUS HARTOG, Queen's College, Cork	583

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MAY, 1903.

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On Planktonetta atlantica, Borgert. By G. HERBERT FOWLER, B.A., Ph.D., F.Z.S. (With Plates 11 and 12)	133

The Genera and Species of the Order Symphyla.

By

H. J. Hansen
(Copenhagen).

With Plates 1—7.

I. HISTORICAL NOTES.

IN 1884 Dr. R. Latzel published the second half of his fine and highly valuable work 'Die Myriopoden der österreichisch-ungarischen Monarchie,' ii, 1884. His treatment of the order Symphyla (pp. 1—18 and Taf. i) is a very important contribution: it contains a rather detailed description of the external structure, abstracts of earlier papers on some of the internal organs, notes on some larval stages, the best descriptions hitherto published of three European species, a sketch of the history of the systematic position of the group, etc. In reality it gives both a considerable addition to our knowledge, and abstracts of or reference to nearly all earlier scientific papers until 1882 touching the subject. I will therefore refer the student to Latzel's book, and confine myself to a very short extract and a few remarks.

We learn that Scopoli in 1763 described the first species of this order, viz. *Scutigera niva*, which he referred to the genus *Scolopendra*.

In 1839 H. P. Gervais described another species, nota-

cantha, upon which he founded the genus *Scolopendrella*, and referred it to the family *Geophilidæ*.

In 1844 Newport discovered the common species *S. immaculata*, and established first the *Scolopendrellinæ* as a sub-family of the *Geophilidæ*, but shortly afterwards as a family near the *Lithobiidæ*.

In 1880 F. A. Ryder made an important step, raising the group to the rank of a separate order, to which he gave the well-chosen name, *Symphyla*, and in 1882 he divided it into two genera, *Scolopendrella*, Gerv., and a new one, *Scutigereila*, Ryder.

From 1873 to 1882 European and American zoologists had established some new species, but in the treatment of Latzel they have all been withdrawn as synonyms of the three species mentioned above. At the end of 1882 not more than three species were known from the whole world, but it must be added that at least one of the species cancelled, *S. microcolpa*, Muhr (and possibly also *S. gratiæ*, Ryder), must be re-established as valid, and that the form described by Latzel as *S. notacantha*, Gerv., var. *munda*, is not this species (see the next page). To give a more detailed review, with critical remarks, of the contents of Latzel's treatment is, in my opinion, not necessary, especially as some points will be mentioned in the following pages.

In 1883 S. Scudder established a new North American species, *S. latipes*, which certainly is dead-born (see later on).

In 1886 B. Grassi published his important paper, "*Morfologia delle Scolopendrelle*" ('*Mem. d. Reale Accad. d. Scienze di Torino*,' Ser. 2 a, T. xxxvii, pp. 593—624, Tav. i, ii). The author begins with a description of four Italian species known to him: *S. immaculata*, Newp., *S. nivea*, Scop., *S. notacantha*, Gerv., and a new form, *S. Isabellæ*, Grassi. He states correctly that *S. notacantha*, Gerv., has the first pair of legs "relativamente corto" and simple setæ on the antennæ; furthermore that the species described by Latzel as *S. notacantha* is not

referable to that species. He has examined specimens which, in his opinion, belong to *S. notacantha*, Latz., and on these specimens he establishes his new *S. Isabellæ*, which, above all, is distinguished from *S. notacantha*, Gerv., by having only eleven pairs of legs, whereas twelve pairs are found in the last-named species. In *S. Isabellæ* he has discovered "una papilla brevissima" furnished with hairs, without claws, and not divided into joints, placed on the latero-ventral part of the first segment of the trunk, and he thinks that its distance from the median line is so long that it cannot easily be considered as homologous with the first pair of legs in *S. notacantha*, Gerv. But in *Scol. Silvestrii*, n. sp., described below, the first pair of legs have as many joints as in *S. notacantha*, Gerv., but they are much shorter and inserted as the "papilla" in *S. Isabellæ*, and it must be taken as granted that the wart-like protuberance in the last named, and in several other species, is a very reduced leg; it is also present in specimens in which the posterior pairs of legs have not yet been developed. The existence of this pair of wart-like legs separates *S. Isabellæ* sharply from *S. notacantha*, Gerv., but I have studied two rather closely allied Italian species which both possess the characters pointed out by Grassi for his *S. Isabellæ*; in all probability he has examined specimens of both species, and not wishing to suppress the name given by him I have retained it for the largest of the two species, which also seems to be common at Catania.

Grassi spends ten pages on the external and internal anatomy, but I will only mention two points. His treatment of the sense-organs is rather incomplete; in *Scut. immaculata* and *nivea* he has seen none of the organs of the antennæ described below. His description of the mouth-parts is rather good (the figures unfortunately poor), and it must be emphasised that he points out mandibles, maxillæ, labium (composed "di un semilabbro destro e di uno sinistro"), and a hypopharynx consisting of a ligula and two paraglossæ; a comparison of his interpretations with

those set forth by me in a following chapter will show that I have accepted them as quite correct, with exception of his opinion on the "paraglossæ." His very long discussion (pp. 607—617) on the affinities of the order must be passed by here, but it may be added that he gives a not quite complete list of the papers printed between 1763 and 1885, in which *Scolopendrella* has been mentioned.

In 1889 Dr. E. Haase published his well-known paper "Die Abdominalanhänge der Insekten, mit Berücksichtigung der Myriopoden" ('Morphol. Jahrb.,' B. xv, pp. 331—435, Taf. xiv, xv), in which he investigates and discusses the appendages at the base of the legs and the ventral sacs.

In 1895 P. Schmidt published "Beiträge für Kenntniss der niederen Myriopoden" ('Zeitschr. f. wiss. Zool.,' Bd. lix); the morphology of *Scolopendrella* is dealt with on pp. 461—78 (Taf. xxxvii, figs. 31—45), and some of the anatomical results do not agree with those of Grassi, but the paper contains nearly nothing of any significance to the purpose of the present paper. Schmidt states that he has examined *S. immaculata*, captured partly near St. Petersburg, and partly in the orangery of the botanical gardens in that town, but I am inclined to suppose that the animals from the orangery belonged to the species described later on as *Scut. caldaria*, n. sp.

From 1885 to 1900 several zoologists—E. Haase, E. Daday, A. Berlese, C. v. Porat, and C. Graf v. Attems—have re-described earlier known species of *Symphyla* collected in the European countries of the respective authors, or published local faunistic lists; and A. S. Packard, R. I. Pocock, and F. Silvestri have indicated new localities out of Europe for *Scut. immaculata*. In another chapter of this treatise the most interesting localities, stated in some of the papers of these authors, for the last-named species will be discussed, while the other localities and the descriptions need no mention. Since Grassi's paper (1886) no author has established any species or genus of our order.

It may be proper to conclude with a short review. Of the

order, four European species are at present admitted, but one of them, *S. Isabellæ*, is collective; a fifth species, *Scol. microcolpa*, Muhr, has incorrectly been withdrawn by Muhr himself one year after its erection, and subsequently by Latzel and the other authors. In North America four species have been found, and two of them described as new, viz. *S. latipes*, Scud., which must be cancelled, and *S. gratiæ*, Ryder, which has been withdrawn by Latzel as synonymous with the European *S. nivea*, Scop., but I cannot decide if this withdrawing is correct. From other parts of the world no new species has been described. The result is that of the species established from the whole world and admitted as valid by the best authors in papers since 1884 (this year included), only three European species have been described so that they can be recognised with tolerable certainty, and a fourth one is collective. It may, perhaps, be admitted that in the 138 years elapsed since *S. nivea* was described the progress of our study of the forms of this highly interesting order, which certainly contains at least more than 100 species, has been rather slow.

II. THE MATERIAL AND ITS TREATMENT.

The material examined by me is comparatively very rich, consisting of some hundreds of specimens collected in several countries of Europe, in Algeria and the Cape Colony, in Texas, in various countries in South America, as Venezuela, Chile, and southern Brazils to southern Patagonia, in Java, Sumatra, and Siam; twenty-four species are described.¹ The major part of the specimens and species belong to the Copenhagen Museum; most of the animals from Europe have been captured by the author, who collected seven species in Calabria in May and June, 1893, and one species besides in

¹ Two new species, one from Temuco in Chile and one from the island of Koh Chang (Gulf of Siam), have been omitted; of each I had only one badly preserved specimen.

hothouses in Copenhagen; eight new species have been collected by two other Danish zoologists, viz. three by Dr. F. Meinert in Algeria and Venezuela, and five species by Dr. Th. Mortensen in Siam; it may be added that it was the arrival in 1900 of the fine collection secured by Dr. Mortensen which induced me to study the Palpigradi, Pauropoda, and Symphyla. On my request Dr. F. Silvestri kindly lent me a good collection, especially all the animals described here from the southern countries of South America; furthermore, specimens have been benevolently sent me by the Director, Prof. E. Ray Lankester, from the British Museum, by Prof. E. L. Bouvier from the Museum in Paris, by Prof. Max Weber from the Museum in Amsterdam, by Mr. R. I. Pocock (London), Mr. Carl Börner (Marburg), and Prof. W. M. Wheeler (Austin, Texas). I beg all these gentlemen to accept my sincere thanks for their valuable aid.

The collectors of Symphyla should put the animals in spirit of about 63 per cent., and at most not exceeding 70 per cent. When the specimens are to be examined they must be put in glycerine somewhat diluted with water on the object-glass, and the glass-cover ought to be supported by a small wooden wedge to prevent flattening of the specimens; I have described my method in the paper on the Pauropoda ('Videnskab. Meddelelser fra den Naturh. Forening i Kjöbenhavn' for 1901, published March, 1902), and refer the readers to the chapter in question (pp. 327, 328). The animals must be examined both vertically from above and from the side, and it is often necessary to use a comparatively high magnifying power (200 to 500 times). The real shape and relative length of the claws are often difficult enough to observe, and in order to produce correct drawings I have generally found it necessary to cut off the left leg of the twelfth pair (if this was broken the penultimate leg was chosen) and one of the first pair, if this is well developed: often I also cut off the right leg of the last pair to examine and draw the claws from the inner (the posterior) side as those of the other leg. A glance on the plates will show that of nearly all species I have drawn the

same leg and the same claws in the same position in order to facilitate a direct comparison of the shape, etc., of the parts in question. Furthermore, the legs of the last pair, the legs of the first pair if these are not quite rudimentary, and the cerci have always been drawn with the same degree of enlargement, the claws of the first and the last pairs of legs with a higher degree, which is identical for both figures; the result of these arrangements is that the figures also show the proportions as to length, etc., between the cerci and the legs mentioned of each species. (Of course, it has been impossible to draw the legs and cerci of a small and of a large species with the same degree of enlargement, for the figures of the large species would be enormous if those of the small one should be really useful and not too small.) I should advise future students of this order—and of many other groups—to follow a similar plan when drawing figures.

III. ON SOME STRUCTURAL FEATURES AND CHARACTERS.

A. Variation.—It may be practical to begin with some remarks on this topic. During a preliminary study I was induced to think that it would be rather easy to separate and describe nearly all the species of the genus *Scutigere*lla, as they presented several characters, whereas the other genus, *Scolopendrella*, seemed to be more difficult; but later on I arrived at the opposite result. The species of the last-named genus show several characters, and most of the features which differ from each other in all or nearly all species present only a slight or no variation in specimens with the full number of legs of the same species. In *Scutigere*lla, at least, several species show a special difficulty: specimens of the same species having acquired the full number of legs vary very much in size; this difference can be very large between specimens from the same locality or from different localities, and arises often, most probably, from the age of the individuals; but sometimes it is a real local variation, a remark already set

forth by Latzel on *Scut. immaculata* in Austria. This variation in size is connected with differences in certain parts presenting specific characters, and two striking examples may be pointed out here. In very large specimens of *Scut. immaculata* the cerci are about six times, whereas in a small specimen they were only four times longer than deep, thus considerably more slender in large than in small individuals. In large specimens of *Scut. angulosa*, n. sp., the last pair of legs—and to a little lesser degree the penultimate pair, and to a somewhat lesser degree the antepenultimate pair—are more robust and widened, especially in the proximal portion of their tarsi (Pl. 4, fig. 2 *e*) in a way which at least very rarely is met with in small specimens (comp. Pl. 4, fig. 2 *k*, with fig. 3 *e*, and the explanation of the plate). A similar difference has been observed between the shape of the posterior pairs of legs in a large and in a small specimen of *Scut. capensis*, while in several other species no such difference has been found. Such variation in structural features, generally but not even always proportionate to the size of the specimens, can be very perplexing, and in some cases it is very difficult or perhaps impossible to distinguish with absolute certainty between variety and species without having a rich and well-preserved material from many localities. The genus *Scutigerella* has caused me much trouble, and I may advise future students not to establish new species without a very careful and prolonged examination of several forms, and never to establish a species on specimens not having acquired the full number of legs, or on specimens in which the legs of the twelfth pair are not quite as long and do not possess so many setæ as those of the eleventh pair.

b. Head.—It is comparatively shorter and broader (and thicker) in *Scutigerella* than in *Scolopendrella*, but the proportions between the dimensions in question vary conspicuously between the species of the same genus. While the breadth is easy to measure when the animals are seen from above, the length can often only be measured with accuracy when they are seen from the side; I have often not found it

necessary to give the exact proportion between the length and breadth in the various species, but only an estimate. The length of one pair of lateral setæ as compared with the breadth of the proximal joints of the antennæ is a character in *Scutigere*lla. It is well known that internal linear thickenings of the dorsal integument have been observed in European species; the thickening in the median line I name the central rod; from the anterior and posterior ends of this a pair of branches originate. The major part of this structure is much more easily seen in *Scolopendrella* than in the other genus, and it presents a few characters used in the descriptions below. The eye-spots have been omitted as nearly valueless.

c. Antennæ.—Latzel especially has pointed out with his usual accuracy that in the three species known to him the number of joints varies very much in specimens of each species, and above all in *Scut. immaculata*, in which he has found from eighteen to fifty-five joints. The degree of variation is, on the whole, considerably larger in *Scutigere*lla than in *Scolopendrella*. Notwithstanding this, the number of joints is not quite worthless, as it is considerably higher in some species than in others. The shape of the joints is generally without any significance, as it in reality is rather uniform in nearly all species of the same genus, and besides presents too much difference according to the degree of contraction of the antennæ. Sometimes this contraction is so considerable that the distal part of many joints is concave instead of conically truncate, and in this case the antennæ show a very anomalous appearance, the joints being only half as long as usual, but considerably thicker than in their normal state, much resembling cups arranged in a pile. Only in two species, *Scut. crassicornis* and *Scut. pauperata*, the subproximal part of the antennæ has the joints really thickened in proportion to the rest (Pl. 4, fig. 4*a*). Each joint, the terminal one excepted, has always a whorl of stiff setæ on the thickest part; the setæ in this whorl, which I name the central one, differ somewhat in length in the different species, and in *Scut. crassicornis* and *S. pauperata* the setæ on the inner (anterior)

side (Pl. 4, fig. 4*b*) of the thickened joints are very elongate and vertical on the antennal axis. In most species these setæ are slender, slightly conical, and naked, but in two species of *Scolopendrella* (*Scut. microcolpa*, Muhr, and *Scut. antennata*, n. sp.) nearly all the setæ are much thicker and adorned with very conspicuous branches on all sides (Pl. 5, fig. 4*b*, and Pl. 7, figs. 6*a*—6*c*). In all species at least one secondary whorl of shorter setæ has been partly or fully developed behind the central one, at all events in the most distal joints. In most species of *Scutigera* and some species of *Scolopendrella* a third whorl is developed behind the second one or between this and the central one, at least on the lower side of the distal joints, and a rudiment of a fourth can sometimes be found. On the upper side of the distal joints a part or a rudiment of a whorl of fine and short hairs or setæ is found in advance of the central one. The degree of development of the whorls on the proximal, middle, and distal parts of the antennæ present specific characters.

In *Scutigera* I have discovered various sense-organs on the antennæ. In all species the terminal joint has on its distal surface at least one organ—generally two or three organs,—and these differ often, but not always, considerably in size. An organ of this kind consists of a stalk which is either short or rather long, often gradually increasing in thickness outwards, and from its end originate four fine branches which are slightly convex outwards, subparallel or slightly diverging, and certainly always united by a very thin, clear membrane. A large organ of this kind, a striped organ, placed on a wart-like protuberance in *Scut. unguiculata*, is shown in Pl. 2, fig. 2*c*; fig. 2*b* on Pl. 4 (in *Scut. angulosa*) shows a large organ and a smaller one with the branches feebly developed. Fig. 2*b* on Pl. 5 represents the terminal joint of *Scut. pauperata* with two organs (more magnified in fig. 2*c*), one with branches in the membrane, the other thicker, more rounded, without separate stalk, and without branches. Fig. 2*b* on Pl. 4 shows not only two striped organs, but between the normal setæ subcylindrical rods,

which probably also are a kind of sense-organs, and exist in some and perhaps in all species of the genus. On the upper side of most of the joints, the proximal ones excepted, is generally found a very small organ with the branches mentioned, and at least in one species two organs of this kind. In *Scut. crassicornis*, n. sp., and *Scut. pauperata*, n. sp., there is besides on the same joints near the upper organs a single, rather thick, conical rod; in other species this rod is very slender, often not easily discernible from a normal short seta, and in *Scut. angulosa* some slender sub-cylindrical rods with the end acuminate are found together with the fine setæ mentioned above in advance of the central whorl on the distal joints. The quality and number of all these organs present at least sometimes, and probably always, specific characters to a certain extent. Some points are briefly mentioned in the descriptions below, but a more detailed study than I was able to undertake is needed.

In *Scolopendrella notacantha*, Gerv., I have observed two organs of the striped sort on the end of the terminal joint. In *Scol. Isabellæ* organs of a very different kind were present on the same surface, but these organs are so small that an enlargement of 600 times is quite insufficient, and I have been compelled to give up the searching for sense-organs in species of the genus *Scolopendrella*.

D. Dorsal Scuta.—The tergum belonging to the segment bearing the first pair of legs is rather or very short, and never developed as a real scutum like the following ones; I have therefore found it practical not to include it in the sum of the scuta; when in the descriptions of the species the second scutum is mentioned I mean the second of the large, real scuta. It is well known that in all Symphyla the number of such scuta is a little higher than that of the pairs of legs. In *Scutigerebella* they are very easy to count; fourteen scuta are present in all species; they are sharply defined on the sides and especially behind, where a scutum in somewhat contracted specimens overlaps the most anterior part of the following one. In a very extended specimen of

Scut. capensis I observed that all scuta (the first one perhaps excepted) are divided by a transverse furrow into a very short anterior and a long posterior part; the anterior part is in this species easily distinguished from the articulating membrane in front of it by its surface, which is adorned with short, irregular, somewhat curved, transverse stripes, while the articular membrane wants such stripes, but is finely dotted. In very extended specimens of other species I have found a similar division of the scuta, but the anterior part is here often scarcely distinguishable from the articulating membrane. The species of *Scolopendrella* possess also fourteen scuta, but the two posterior ones are divided by a transverse stripe of articulating membrane, so that they can easily be counted as four scuta, the anterior part being more than half but scarcely ever quite as long as the posterior one; the anterior parts are setiferous like the others, but are easily distinguished by their shape; all the scuta, the fourteenth one excepted, are posteriorly produced into two lateral triangular plates of considerable size, those of the last one being somewhat smaller, but the hind margin of the anterior part of the two posterior scuta is transverse without any vestige of triangular plates. In very extended specimens of various species it is observed that the first to the twelfth scuta are divided into a long posterior part and an anterior one, which is a little longer than in the other genus, and generally very difficult or impossible to distinguish from the articulating membrane.

In *Scolopendrella* the shape of the posterior triangular plates and their distance from each other differ after a certain rule in the scuta of the same animal; for instance, the plates of the second scutum are always more narrow in proportion to their length and less distant from each other than those of the third scutum (various figures on Pls. 5—7); the plates of the others are rather similar in shape either to those of the second or those of the third scutum, or form a transition between them. I have found these two scuta to be the most practical to study, and the others are omitted as

rather superfluous in the descriptions of the species. The two scuta present excellent specific characters, being not quite similar in any two species, and differing not only as to shape and distance of the triangular plates, but also in the number of marginal setæ on these plates, in the length of the antero-lateral seta, etc., while the individual variation seems to be slight in all respects.

In *Scutigere*lla the scuta present several excellent characters, but not as many as in the other genus. The shape of the posterior margin of all the scuta, the last one excepted, of the same specimen is rather similar in the main features; the last scutum differs in the whole order essentially from the others in shape and endowment with setæ. I have found the second and the penultimate scuta to be more different from each other than the intermediate ones, and these two scuta are therefore described in all species. The marginal setæ of the scuta present good characters, but their length shows some individual variation. A pair of antero-lateral setæ are often especially elongate on the anterior scuta or on nearly all scuta; these setæ are always inserted on the most lateral point of the scutum (consequently where this is broadest); on the anterior scuta this point is situated much in front of the middle, on the posterior scuta behind the middle. When these setæ are especially elongate they are at least on the anterior scuta and sometimes also on the posterior scuta directed outwards and less or more forwards. Furthermore, the longest pair of lateral setæ are generally of importance, and some other small features are mentioned in the descriptions of the species. The last scutum presents a very curious structure in two closely allied species, *Scut. immaculata* (Newp.) and *Scut. armata*, n. sp.: an oblong median area at the hind margin is so deeply impressed or invaginated that a cavity is formed, the anterior part of which is overlapped by the protruding dorsal wall; around this cavity (Pl. 1, fig. 1 c) a belt of the interior tissue shows a peculiar aspect, indicating the existence of an organ which probably is a gland, but a special investigation of the

histological structure has not been undertaken. In two other species, *Scut. crassicornis*, n. sp., and *Scut. pauperata*, n. sp., a deep depression is found, but no invagination, and therefore no cavity, has been developed; the interior tissue shows an organ less distinct than in *Scut. immaculata*. In the other species of *Scutigerella* a feeble and simple depression is observed; in *Scolopendrella* the last scutum is simple.

E. Legs.—The legs of the first pair will be treated separately below. They present always essential structural differences from the eleven other pairs, which in all main points are similar to each other, not only in the same animal but in all species of the order. These eleven pairs consist apparently of five joints. But the proximal one of these joints is, in my opinion, the trochanter, and the coxa can easily be seen as a separate portion of the skeleton on the lower surface of the trunk on a specimen cleaned with caustic potash. That the second one of the five joints mentioned is the femur and the last one is the tarsus is, of course, certain, but the interpretation of the two remaining joints is more difficult. The shape of these joints and the presence of only one condylus placed on the dorsal side seem to indicate that the joints must be interpreted as patella and tibia; on the other hand, the essential movement between the joints being a rather strong flexion in the vertical plane, while the movement forwards and backwards around a sub-vertical axis seems to be feeble, leads to the assumption that the joints are respectively tibia and metatarsus. I think that this last interpretation is correct, and it is supported by the shape of the dorsal condylus, which is unusually broad, and seems to be formed by a junction of two condyli placed closely together. The tarsus terminates in a praetarsus¹ with two claws, which are never quite equal in shape, the anterior claw being always broader, generally

¹ This name has been introduced by N. J. C. H. de Meijere in his paper "Ueber das letzte Glied der Beine bei den Arthropoden" (*Zoolog. Jahrbücher, Abtheil. für Anatomie, etc.*,² Bd. xiv, 1901, pp. 417—476, Taf. 30—37).

conspicuously longer, and scarcely ever shorter than the other. The anterior is inserted on the distal end of the "prætarsus," the other claw on the posterior side of the same joint; the morphological interpretation of the prætarsus and the two claws is that set forth on similar parts in *Japyx solifugus*, in § 51 of my paper "Zur Morphologie der Gliedmassen und Mundtheile bei Crustaceen und Insekten" ('Zool. Anzeiger,' 1893, Nos. 420 u. 421).

The last pair of the legs mentioned present the specific characters especially well developed; the penultimate and antepenultimate pairs can also be used. The length of the tarsus in proportion to its depth, and the number and length of outstanding dorsal setæ both on this joint and on the metatarsus and tibia, present good characters in *Scolopendrella*. In *Scutigerebella* the shape of the tarsus is of lesser value, as it sometimes shows variation between large and small specimens, etc. (see above, and also under the descriptions of the species); the number and the length of the setæ in the anterior dorsal row on metatarsus and tarsus and the length of a distal seta on the tibia are always valuable, though sometimes also presenting variation to a certain degree. The claws of the posterior pairs are important in *Scutigerebella*, but must be studied with caution, as an oblique position of one of the claws under the microscope easily conveys a misleading image. In *Scolopendrella* the claws are less valuable, their difference in various species being generally smaller. It should be emphasised that the last pair of legs must be fully developed, at least quite as large as the preceding pair, and with the number of setæ at least as high as on those legs, otherwise the shape of their tarsi and claws and the number of their dorsal setæ will give misleading results.

Various names have been given to the well-known moveable, protruding organs at the base of each leg of the ten posterior pairs; I will name them exopods, but must abstain from setting forth here an explanation for the choice of this name. These exopods are very short and difficult to discover in all species of *Scolopendrella* and in *Scutigerebella*

pauperata, n. sp., but they are somewhat longer or even rather long in the other species of the last-named genus.

The legs of the first pair are always at least somewhat shorter than the following pair, and instead of tibia and metatarsus only one joint is present between femur and tarsus. In all species of *Scutigera* and in *Scolopendrella notacantha*, Gerv., this first pair are still rather large; in some other species of *Scolopendrella* they are more reduced in size or even short, but the three protruding joints are plainly seen (Pl. 5, fig. 4 *f*; Pl. 6, fig. 3 *e*). In many species of the last-named genus they have been reduced to very small or exceedingly small wart-like protuberances (see, for instance, Pl. 6, figs. 4 *e* and 6 *c*), without any vestige of articulation, without claws, and often very difficult to discover. When these legs are divided into joints the tarsi terminate in two claws, of which the anterior one is generally proportionately more slender and less curved than in the following legs, and the relative length of the claws presents a specific character.

In all legs the *prætarsus* has on the anterior side a single seta, which is much longer than its hairs, and sometimes (*Scut. capensis*, n. sp.) even longer than the claws (Pl. 3, fig. 5 *d*); it is here named the front seta. In the first pair of legs it is sometimes very thick and almost claw-like, which is a good character.

F. *Cerci*.—Both the shape and the furniture with setæ present good characters. At the distal end they are always cut off obliquely, so that a conspicuous flat area is presented; in *Scolopendrella* this area turns downwards or outwards, in *Scutigera* outwards or partially or wholly upwards; its direction is always a good specific character if the natural position of the cerci has not been disturbed by pressure, which is the case in a small percentage of the specimens. Furthermore, in *Scolopendrella* the dimension of this area is valuable. In *Scutigera* neither the area itself nor the surface opposite to it present any stripes; in *Scolopendrella notacantha* the area has a number of somewhat

irregular longitudinal stripes (Pl. 5, fig. 3 *k*), the nature of which is unknown to me; in all the other species of *Scolopendrella* the terminal surface opposite to it shows several transverse lines, which on each side converge to the base of the area, and each of these stripes consists of many exceedingly small spines arranged in a line (Pl. 6, fig. 4 *g*); the area is also generally more or less adorned with longitudinal stripes (Pl. 6, fig. 4 *h*). In all species of *Symphyla* the cerci terminate in one or two setæ. One is very short or sometimes absent, and has been omitted in the descriptions; the other varies from being rather short to exceedingly long.

In *Scolopendrella* the length of the cerci in proportion to the last pair of legs, their length in proportion to their depth and sometimes also to their breadth, the density and length of their clothing, and the length of the apical seta present excellent specific characters; in *Scutigera* the density of their setæ and the length of the distal setæ are always important, but the proportion between length and depth is sometimes less constant, presenting differences in small and large specimens (see especially on page 30 on *Scut. immaculata*).

G. Tactile Hairs on the Last Segment.—The essential structure of these organs has been described by earlier authors. Here I shall only direct attention to the rather different shape, etc., of the calicles mentioned below in the diagnoses of the genera. The length of the tactile setæ is scarcely valuable as specific character.

IV. ON THE MORPHOLOGY OF THE MOUTH-PARTS.

It may perhaps be allowed to insert a short chapter on this matter, though it lies outside the scope of the present paper.

I have examined specimens of *Scutig. immaculata* (Newp.) and *Scolop. vulgaris*, n. sp., two species very distant from each other.

The best results were obtained from preparations cleaned

with caustic potash; the dorsal part of the head and of the two anterior segments of the trunk has been cut off and the lower half put in a cold solution of about 25 per cent., in which it remained during twenty-four hours, and was then put in glycerine on an object-glass. The hypopharynx and the maxillulæ have also been examined by dissection of a head directly taken out of the spirit. The following description is founded almost exclusively on *Scutig. immaculata*; some smaller differences between the structure of this species and of *Scolop. vulgaris* have been observed, but, with the exception of one point, I did not find it necessary to mention them.

The mandibles are two-jointed as in typical Diplopods, but the interpretation of this curious fact must be postponed, and shall be dealt with in a paper on the morphology of the skeleton of some classes of Arthropods. The basal joint (Pl. I, fig. 1 *a*, *a*.) is narrow when seen from below, but rather broad when seen from the outer side; to the upper margin just behind the middle a strong muscle (*b*.) is attached. The distal joint (*c*.) is strongly compressed, its articulation on the basal joint is well developed, and besides, it has on the upper side near the basal margin a strongly prominent part, which seems to be a secondary condylus, a structure difficult to understand. The oblique distal cutting edge is serrated with a moderately deep incision at the middle; in this incision is found a rather small, thin lacinia (fig. 1 *c*, *l*.), articulated to the upper surface of the mandible near the margin of the incision; this lacinia is distally very irregularly and partly deeply serrated, and has, besides, a narrow, nearly setiform process, directed inwards above the adjacent part of the mandible; this lacinia is equally developed both on the right and on the left mandible. To the inner posterior angle of the second joint of the mandible a tendon of a very strong muscle (*d*.) is attached.

The maxillæ (*e*.) are quite independent of the labium, united with it only by a belt of articulating membrane. The "stipes" is long; posteriorly it is bent upwards and ter-

minates there in a short, angular projection, which can be seen from below through the skin; this short, curved part with its angular projection is probably the "cardo" fused with the stipes; a suture between them could not be discovered. As in many insects the two elements forming the stipes have been completely fused; two well-developed lobes proceed from the distal end of the stipes, and a little behind the base of the outer lobe a very short palpus is seen; this palpus (*f.*) consists in *Scutig. immaculata* of one very short joint; in *Scolop. vulgaris* it is twice as long, and consists of two joints. The main points as to shape and quality of the skin of the two lobes can be seen on the figure.

The labium shows a considerable resemblance to that of certain insects. The basal part, the "submentum" in insects, consists of a pair of narrow, well-chitinated plates or rods (*h.*), encompassed on both sides by membranous skin; near the base of a maxilla each of these rods is articulated to a narrow plate proceeding backwards, and these plates (*g.*) are the sternum of the segment to which the labium belongs. (The existence of this segment in Orthoptera has been pointed out by me in the paper on *Hemimerus* ['Entomol. Tidskrift,' Stockholm, Bd. xv, 1894].) The anterior ends of the submentum are articulated to short posterior prominences of the "mentum," a large shield (*i.*), a little longer than broad, and divided in the median line by a narrow stripe of membranous skin into two halves. The distal margin of the mentum is concave, and bears two pairs of rather small lobes (*k.*), well separated by membrane both from the mentum and from each other; besides, the mentum has each anterior outer angle produced into a subtriangular plate on the side of the outer lobe.

The hypopharynx and the maxillulæ are very interesting; my interpretation is in some respects very different from that of other authors. The hypopharynx (fig. 1 *e, h.*) protrudes freely in the mouth above the distal part of the labium as a rather thick, subquadratic prominence; its anterior mar-

gin is convex, and on the upper side near the margin a pair of very broad and very short rounded lobes project freely over the antero-lateral margin, and are a little removed from each other at the middle. At the base of the hypopharynx its upper side shows a transverse linear thickening, which is sinuate, showing one unpaired and one pair of more lateral strong curves turning backwards; near the base of each lateral curve is attached a long and strong narrow plate (fig. 1 *d, p.*) directed backwards, and these two plates are the inner skeleton of the head also met with in lower insects,—for instance, Hemimerus. From each outer angle of the middle curve a chitinous ridge proceeds forward and a little outward supporting the hypopharynx. Outside each of these ridges a maxillula (*m.*) is articulated in the lateral curve of the transverse ridges; this maxillula, which proceeds forwards and somewhat inwards above the upper side of the hypopharynx, is oblong, nearly equal in breadth, with the distal margin cut off obliquely; its wall is rather firmly chitinised in parts, and the distal inner portion is submembranous, hairy, and on the whole showing a structure like that often observed on a lobe of a paired mouth-limb. I consider it to be absolutely certain that these maxillulæ do not belong to the hypopharynx as “paraglossæ” (Grassi), but that they are real mouth-limbs homologous with the first pair of maxillæ in Crustacea and lower Insecta; in 1893 I have (in ‘Zool. Anzeiger’) given the name “maxillulæ” to these mouth-limbs in the classes named.

This not very detailed description of the mouth-parts must be sufficient here; the figures will show several smaller features not mentioned. A special comparison of the mouth-parts of the Symphyla with those in Thysanura, Diplopoda, etc., shall be given in a future paper.

V. ON THE GEOGRAPHICAL DISTRIBUTION.

The enumeration on p. 5 of the countries in which the animals seen by me have been captured is nearly exhaustive as to our present knowledge of the distribution of the order; only the north-easterly part of the United States, North America, Mexico, and India must be added to the list mentioned. But I venture to state that species of this group can be captured in all countries of the world with exception of the arctic and antarctic regions. I have examined twenty-four species, which is six times as many as accepted by the best authorities in the last sixteen years, but I am convinced that nearly one hundred species, and perhaps a considerably higher number, are still undiscovered. The animals are easy to collect, easy and cheap to preserve, the group is of high systematic value, and our knowledge of its species has hitherto been quite rudimentary.

Under such circumstances it is impossible to say much on the geographical distribution, and very few inferences of tolerable certainty can be drawn. I have described twelve species of each of the two old genera; the genus *Scutigera* seems to be distributed a little nearer to the arctic and antarctic regions than *Scolopendrella*. But the species of the last-named genus are generally smaller, and have, therefore, in all probability been more overlooked by most collectors, and judging from this, and from the good result as to new species of the same genus in my own excursions in Calabria, I am inclined to believe that the genus *Scolopendrella* contains considerably more species in warmer regions than *Scutigera*.

Of several species of both genera I have examined specimens from at least two and sometimes from three or more localities rather distant from each other, but the geographical distribution hitherto known of all species, with the exception of *Scutigera immaculata* (Newp.), must be regarded as moderately limited. *Scolopendrella vul-*

garis, n. sp., is free-living in Europe at least from Scilla in Calabria, and probably from Catania (Sicily) to Marburg; in Denmark specimens have been captured in a garden, but not yet in woods. Specimens of *Scol. pusilla*, n. sp., from Palmi and Marburg have been examined; *Scol. notocantha*, Gerv., was established on specimens from Paris, and I have seen specimens from Rome and Calabria; *Scutigerella nivea*, Scop., established on specimens from Bohemia, has been met with in Russian Poland (Latzel), and southwards at least to Palmi in Calabria, and probably to Catania. *Scolop. antennata*, n. sp., has been found in the southern part of Brazil, in Paraguay, and Argentina; *Scutig. angulosa* in Uruguay, and thence to southern Patagonia; *Scutig. orientalis*, n. sp., in Java, Sumatra, and Siam. The distribution of the other species known to me is considerably more restricted, and needs no special mention. Only *Scutig. immaculata* (Newp.) is an exception, though the statements of earlier authors on its occurrence in Chile and Sumatra are later on proved to be incorrect. The species is distributed from 60° lat. N. in Sweden through Europe to Algeria; specimens from Buenos Ayres could not be separated from European individuals, but the supposition that it has been imported with plants from Europe to that city is far from improbable. It is, in my opinion, more puzzling that a few species captured near Austin, in Texas, could not be separated by me with absolute certainty from the European form, and Packard could not find differences between specimens from Mexico and Kentucky, and has besides found it in Massachusetts. The species seems, therefore, to be distributed from Massachusetts, in the north-easterly part of the United States, to Mexico, but it must be added that a careful examination of good material from some localities in Mexico, Texas, and the northern United States is still necessary before the question can be finally settled.

VI. DESCRIPTION OF THE GENERA AND SPECIES.

The group consists of one single family with two genera.¹

In order to facilitate a comparison of the diagnoses of the genera both are placed here.

Gen. 1. *Scutigerella*, Ryder, 1882.

(‘Proc. Un. States Nat. Mus.,’ vol. v, 1882, p. 234.)

The posterior margin of thirteen dorsal scuta (all scuta with exception of the last one) is either slightly convex or emarginate, the lobes on each side of the middle of the emargination often broadly rounded, rarely angular, and in this case several times broader than long.

The head is posteriorly at the middle sharply defined from the neck; the two short rods converging to the posterior end of the central rod are at most moderately developed.

The anterior surface of the posterior pair of legs with a considerable or large number of setæ.

The cerci without stripes on the terminal area, and without transverse lines on the most distal part outside that area.

The sense-calicles near the base of the cerci very irregular, the anterior and lateral parts of its wall being vertical and the posterior part very oblique; a large portion of the margin of the

¹ Some zoologist will perhaps soon establish these genera as families, and divide each of them into two or more genera. In our present state of knowledge I disapprove such proceeding. Many authors are, in my opinion, too liable to subdivide into families and genera, with the result that it is often later on, when many new forms have been discovered, found necessary to establish new and often badly defined genera, etc., in order to bring about equivalence; and it is more easy to establish bad genera than to get them cancelled definitely again.

calicles with many short and generally branched setæ (Pl. 1, figs. 1 *f*—1 *h*; Pl. 2, fig. 3 *g*).

The first pair of legs always well developed and more than half as long as the following pair.

The exopods generally well developed and very conspicuous, rarely very short.

Gen. 2. Scolopendrella, Gervais, 1839.

(‘Comptes-rendus de l’Académie des Sciences,’ T. ix, 1839, p. 532.)

The posterior margin of the thirteen dorsal scuta (all with exception of the last one) produced into a pair of triangular plates, of which several are at most somewhat broader than long and all rather large, with exception of the thirteenth pair.

The head is posteriorly at the middle badly defined from the neck; apparently it is defined by the two short rods converging to the posterior end of the central rod, and these rods are strong and very conspicuous.

The anterior surface of the posterior pairs of legs with few setæ.

The cerci either with stripes on the terminal area or—generally—besides with elevated transverse lines on the most distal part outside this area.

The sense-calicles near the base of the cerci regular, with the wall vertical on all sides; the margin of the calicles quite naked (Pl. 5, fig. 4 *h*).

The first pair of legs rarely more than half as long as the following pair, often rudimentary, consisting of a small knob-shaped joint without claws.

The exopods always short or even rudimentary.

In these diagnoses I have put forward all the characters which could be rather sharply expressed. The species of

Scutigerella are clothed with a larger number of hairs than those of the other genus; furthermore, the setæ on the antennæ are longer, the branched sense-organs on the last antennal joint are much larger, the central rod in the head is anteriorly less developed and often partly inconspicuous, while it is well developed in Scolopendrella, the fine and short hairs on the legs are somewhat longer and more conspicuous than in the last-named genus. The species of Scutigerella generally acquire a more considerable length than those of Scolopendrella. On the geographical distribution of the genera see above on pp. 21, 22.

Gen. 1. Scutigerella, Ryder.

CONSPECTUS OF THE SPECIES.

It may be practical first to divide the species into three sharply defined groups, and then to give a conspectus of the species of each group.

A. The last dorsal scutum posteriorly with a very deep and rather large median, anteriorly overlapped cavity. The second scutum with the antero-lateral setæ directed essentially backwards and much shorter than the breadth of the proximal antennal joint Group I.

B. The last dorsal scutum posteriorly cut off without any median cavity, at most with a simple depression. The second scutum with the antero-lateral setæ directed straight outwards or even somewhat forwards, and at least nearly as long as the breadth of the proximal antennal joint.

a. The setæ on the inner side of the proximal antennal joints directed obliquely forwards, and, at most, nearly one half longer than the setæ on the outer side. The exopods of the posterior legs well developed, as long as or longer than the depth of the tarsi. The last scutum slightly depressed posteriorly along the middle Group II.

b. Some setæ on the proximal antennal joints nearly vertical to the longitudinal axis of the antennæ and besides

very elongate, the longest of them at least two and a half times longer than the setæ on the outer side. The exopods of the posterior legs short or very short, considerably or much shorter than the depth of the tarsi. The last scutum deeply depressed posteriorly along the middle. Group III.

Species of Group I.

a. The femur of the first pair of legs without any process.

1. *S. immaculata* (Newp.).

b. The femur of the first pair of legs with a conspicuous, oblong, and distally rounded process on the lower side.

2. *S. armata*, n. sp.

Species of Group II.

a. The second scutum with the antero-lateral setæ much (generally twice) longer than any of the lateral setæ, and these are all directed essentially backwards.

a. The setæ on the cerci very numerous, all rather short, and the distal ones not half as long as the depth of the cerci.

§. The posterior pairs of legs with the anterior claw, especially its distal slender part, very elongate, while the other claw is of normal length and very slender.

3. *S. unguiculata*, n. sp.

§§. The posterior pairs of legs with the anterior claw at most of moderate length, while the other is of normal depth.

x. The central whorl on the antennal joints with the setæ rather short and those on the lower side considerably shorter than on the upper. The first pair of legs with the posterior claw a little more than half as long as the other.

4. *S. caldaria*, n. sp.

xx. The central whorl on the antennal joints with the setæ rather long and those on the lower side only a little shorter than on the upper. The first pair of legs with the posterior claw not half as long as the other. 5. *S. orientalis*, n. sp.

β. The setæ on the cerci moderately numerous or few, the most distal ones at least about two thirds as long as the depth of the cerci.

§. The cerci with moderately numerous setæ and the distal ones somewhat shorter than the depth of the cerci. The metatarsus of the last pair of legs with four setæ in the anterior dorsal row, and these setæ scarcely half as long as the depth of the joint . . . 6. *S. plebeia*, n. sp.

§§. The cerci with few setæ and some of the distal ones longer than the depth of the cerci. The metatarsus of the last pair of legs (at least in small specimens) with two setæ in the anterior dorsal row, and these setæ only a little shorter than the depth of the joint . . . 7. *S. nivea* (Scop.).

b. The second scutum with the antero-lateral setæ not longer, often considerably shorter than a lateral pair, which also are directed outwards and generally besides somewhat forwards.

a. The second scutum with the hind margin slightly convex in its middle half, and without vestige of angles.

§. The metatarsus of the last pair of legs with the distal dorsal setæ long, and one of them at least as long as the depth of the joint; the tarsus with some of the dorsal setæ as long as the depth of the tarsus. The cerci at most five times longer than deep . . . 8. *S. chilensis*, n. sp.

§§. The metatarsus and tarsus of the last pair of legs with all setæ rather short. The cerci more than five times longer than deep . . . 9. *S. capensis*, n. sp.

β. The second scutum with the hind margin rather deeply emarginate, and the lobes on each side posteriorly angular.

10. *S. angulosa*, n. sp.

Species of Group III.

a. The second scutum with the hind margin deeply emarginate and the emargination angular in the median line; its antero-lateral setæ only nearly as long as the breadth of the proximal antennal joints. The last pair of legs with none

of the dorsal setæ half as long as the depth of the metatarsus.

11. *S. crassicornis*, n. sp.

b. The second scutum with the hind margin flatly emarginate, the emargination not angular in the median line; its antero-lateral setæ very long, much longer than the breadth of the proximal antennal joints. The last pair of legs with a dorsal seta on the metatarsus two thirds as long as the depth of this joint 12. *S. pauperata*, n. sp.

GROUP I.

1. *Scutigera immaculata* (Newport). Pl. 1, figs. 1*a*—1*v*, 2*a*—2*f*, 3*a*—3*h*.

1845. *Scolopendrella immaculata*, Newport, 'Transact. Linn. Soc. Lond.,' vol. xix, p. 374, pl. xl, figs. 4*a*, *b*, *c*.

1851. *S. immaculata*, Menge, 'Neueste Schrift d. naturf. Ges. Danzig,' iv, H. 4, ii, p. 13, Taf. i, figs. 24—29; Taf. ii, figs. 1—26.

1871. *S. immaculata*, Packard, 'Amer. Naturalist,' xv, p. 700, figs. 1—1*e*.

1884. *S. immaculata*, Latzel, 'Die Myriop. d. öster.-ungar. Monarchie,' ii, p. 15, Taf. i, figs. 3—9.

1885. *S. immaculata*, Berlese, 'Acari, Myriopoda et Scorpiones hucusque in Italia rep.,' fasc. xxi, No. 9.

1886. *S. immaculata*, Grassi, 'Mem. d. Reale Accad. d. Sci. di Torino,' ser. 2^a, T. xxxvii, p. 594, Tav. ii (several figures).

(In this list only the more essential descriptions have been included; Latzel gives a complete synonymy until 1882, and since that year the species has been mentioned or shortly described by several authors.)

Material.—Many specimens from several countries in Europe and from Algeria. I have examined also specimens from Buenos Ayres and from Austin, Texas, and these will be treated separately under "Variation."

Head.—Moderately broad. The lateral margin rounded

or feebly angular behind the mandible. The seta inserted in front of the posterior end of the mandible is longer than the breadth of the basal antennal joint. The central rod is conspicuous in its whole length, with moderately robust frontal branches, posteriorly connected with a triangular area, without distinct oblique rods, at the hind margin of the head.

Antennæ.—According to my own experience the joints vary from nineteen to fifty; Latzel states the variation to be even from eighteen to fifty-five. The second whorl begins on the lower side before or at the end of the first third of the antennæ, and shortly afterwards on the upper side (fig. 1 *i*); on the distal half, or at least the distal third of the antennæ the secondary whorl is complete on the outer side, and at least one seta of a third whorl is found on the lower side; the setæ in the whorls are rather long. The terminal joint with a rather long striped organ, one or two small organs of the same quality, and some shorter fine hairs among the common setæ.

Scuta.—The second scutum (fig. 1 *k*) posteriorly rather deeply emarginate; the bottom of the emargination not angular but curved, and the broad posterior lobes rounded without vestige of any angle; an antero-lateral seta can often be pointed out, but is always much shorter than the breadth of the proximal antennal joint and directed essentially backwards; the other marginal setæ vary from rather to very short. The thirteenth scutum is sometimes shaped nearly as the second, but often (fig. 1 *l*) it has a more or less deep incision into each posterior lobe; in this case the shape of the twelfth and eleventh scuta presents transition forms between the penultimate scutum and the anterior scuta shaped as the second one. The last scutum (fig. 1 *l*) posteriorly with the characteristic median cavity described above on p. 13.

Legs.—The last pair (fig. 1 *m*) has the tarsus somewhat widened, three and a half to four times longer than deep; the setæ along the dorsal margin of the tibia, metatarsus, and tarsus are short, five to six in the outer row on the

metatarsus, and six or seven in the same row on the tarsus; the anterior claw (fig. 1 *n*) a little or somewhat longer than the other, which is more curved and somewhat more slender, and both claws are elongate. The exopod is long, slightly shorter than the depth of the metatarsus. The first pair (fig. 1 *o*) with the femur simple, without ventral process; the claws (fig. 1 *p*) are elongate, subsimilar in shape, somewhat curved, rather slender, and the anterior one somewhat longer than the other; the front seta is rather long and robust, regularly setiform. (In a specimen with the twelfth pair [fig. 1 *r*] of legs a little smaller than the eleventh [fig. 1 *t*], the pair named has the tarsus three times longer than deep, the dorsal setæ longer, three in the anterior row on the metatarsus, and four on the tarsus, the claws [fig. 1 *s*] shorter, more robust, subsimilar in shape and length, the first pair of legs with the claws [fig. 1 *u*] considerably thicker and shorter than in full-grown specimens.)

Cerci (fig. 1 *q*).—They are adorned with a large number of short and moderately thin setæ; the terminal area is unusually short and looks outwards; the apical seta is rather short, at most half as long as the depth of the cerci. In the largest specimen seen the cerci are six times longer than deep, thus very elongate; in a small but completely developed specimen the cerci are four times, and in all other adult specimens between four and six times longer than deep. (In a specimen with the twelfth pair of legs a little smaller than the eleventh the cerci [fig. 1 *v*] are scarcely three and a half times longer than deep, the number of their setæ is very moderate, and the terminal area looks upwards.)

Length.—Specimens with the last pair of legs well developed that I have seen vary from 3·2 to 7·5 mm. in length; the specimen with the last pair of legs not quite full-grown measures 2·8 mm. According to Latzel the length varies even between 2·5 and 8 mm.

Locality.—In Denmark the species is common in moderately damp places in forests (in old stumps, under moss, etc.); I have also seen specimens from Sweden (collected by

Dr. A. Stuxberg), England (Devonshire, coll. by Mr. R. I. Pocock), Germany (Marburg, coll. by Mr. C. Börner), Austria (Razzes, in Tyrol, coll. by Dr. F. Meinert), France (Meudon and Arques, coll. by Prof. E. L. Bouvier), Italy (Rome, coll. by Dr. F. Silvestri; Scilla, Palmi, and Aspromonte, in Calabria, coll. by myself), Algeria (Bona, coll. by Dr. F. Meinert; Régions des Dayas, coll. by Mr. F. Lesne). Latzel says he has seen specimens from Russia; C. v. Porat (in 'Entom. Tidskr. Stockholm,' 1887, p. 39, and 1889, p. 48) enumerates several localities in the southern part of Norway and Sweden, northwards to Christiania and Upsala, at about 60° lat. N. The species is evidently common from the southern part of Sweden through the whole of Europe to Algeria.

Variation and Probable Geographical Distribution out of Europe.—A large specimen from Denmark measures 5.4 mm. The specimens from Bona are large, and one of them is the largest individual seen by me, but it is only slightly longer than specimens from Rome; the Algerian specimens agree completely with those from Europe. Fifteen specimens captured by Dr. F. Silvestri, and labelled Buenos Ayres, August 7th, 1898, could not be distinguished with certainty from European individuals. The largest South American specimen measures 5.4 mm. in length; its claws on the first and on the last pairs of legs are shown in figs. 2 *b* and 2 *a*; the claws of the same pairs, the twelfth leg, and the cercus of the left side of a specimen measuring 3.5 mm. are shown in figs. 2 *c*—2 *f*; the differences between these parts and the same of the European specimens shown in figs. 1 *m*—1 *u* are probably casual or originating from local variation. Furthermore, I have examined a few specimens captured by Prof. W. M. Wheeler at Austin, Texas; the largest specimen is 5.7 mm., but the others are rather small. The large specimen differs essentially from European forms by the posterior claw (fig. 3 *a*) on the last pair of legs being more robust than in these, and besides almost longer than the anterior claw, which is shorter and more curved than in Danish specimens; the claws on the first pair of legs differ

also (fig. 3 *b*), and are more similar to those in subadult specimens; the claws in the smaller specimens from Austin are somewhat shorter (figs. 3 *e* and 3 *g*) than those of the large specimen, but otherwise agreeing with them. I cannot discover other differences worth mentioning between European specimens and those from Texas (the cerci of the large and of a small specimen are shown in figs. 3 *e* and 3 *h*), but my material from the last-named locality is very scanty and not very well preserved, so that I cannot decide with certainty if the differences mentioned in the claws of European specimens and of the well-grown specimen from Texas are of any importance. I think it necessary to consider the specimens from Texas as probably belonging to *S. immaculata*, but this result may perhaps one day turn out to be wrong.

In 1881 A. S. Packard (op. cit.) stated that specimens taken by him at Salem, Massachusetts, and near the Mammoth Cave, Kentucky, differed from specimens from Bohemia only by "rather longer and slenderer antennæ." In 1886 the same author stated ('Amer. Naturalist,' 1886, p. 383) that specimens from Cordova in Mexico differed from individuals from the United States by being larger (5 mm.) and by having some joints more in the antennæ, and the cerci "slightly longer," but otherwise agreeing with these. His specimens from Mexico certainly belong to the same species as my specimens from Texas, but whether the animals from these subtropical countries differ from the specimens living in Massachusetts, etc., or such northern American animals from European specimens, a future student must decide.

Dr. F. Silvestri writes ('Zool. Anzeiger,' 1899, p. 370) that he found *S. immaculata* abundantly in Chile on his voyage from Temuco to Villa Rica, but specimens captured by him at Temuco and S. Vicente and examined by me belong to *Scut. chilensis*, n. sp.¹ The specimens captured by Prof. Max Weber in Java and Sumatra, and determined by R. I.

¹ One of the specimens belongs to a species unknown to me, but the animal is so badly preserved that I did not venture to describe it.

Pocock as *S. immaculata* ('Zool. Ergebn. einer Reise in Niederl. Ost-Indien,' herausgeg. von Max Weber, B. iii, 1894, p. 319), belong all to another species, *Scut. orientalis*, n. sp. Chile, Java, and Sumatra must therefore be omitted from the countries in which *S. immaculata* has been captured.

Remarks.—The species is easily distinguished from all following species, with exception of *S. armata*, by the characters pointed out on p. 25 for Group I, by the shape of the second dorsal scutum, and by the short setæ and the short terminal area on the cerci.

2. *Scutigerella armata*, n. sp. Pl. 2, figs. 1*a*—1*f*.

Material.—Several species, partly well preserved, from various localities.

Description.—The species is so closely allied to *S. immaculata*, and similar to small or middle-sized specimens of this form, that a few remarks are sufficient. The head and the antennæ present no differences; the highest number of antennal joints observed is thirty-one. The scuta as in the preceding species, but the penultimate scutum has its two posterior lobes equally rounded without incision. The last pair of legs about as in *S. immaculata*; the claws of large specimens (fig. 1*b*) with the distal part of moderate length and slender, the anterior claw rather considerably longer than the other. The first pair of legs (fig. 1*c*) have on the lower side of the femur a very conspicuous vertical process, which is from one and a half times to more than three times longer than thick (figs. 1*d* and 1*e*), subcylindrical, or distally somewhat conical with the apex rounded; the claws of these legs (fig. 1*f*) essentially as in smaller specimens of *S. immaculata*. The cerci also as in that species, in the largest specimen four and a half times longer than deep.

Length.—The largest specimen measures 4·8 mm.

Locality.—Algeria: Bona, five specimens among several of *S. immaculata* (Dr. F. Meinert); Ravin de la Femme Sauvage, end of December, 1892, one specimen; La Bonzarea,

near Algiers, March 19th, 1893, one specimen; Frais Vallon, December 5th, 1892, one specimen; Gorge de la Chiffa, March 5th, 1893, one specimen. The specimens from the four last-named places are all small; they have been collected by Mr. F. Lesne, and belong to the Museum in Paris.

Remarks.—The existence of the process on the femur seems to be the only really sharp character separating this species from *S. immaculata*, but this process, not met with in any other species known to me, is, in my opinion, an interesting and good character, and I must consider the form possessing it as a valid species.

GROUP II.

3. *Scutigerella unguiculata*, n. sp. Pl. 2, figs. 2*a*—2*k*.

Material.—Nearly fifty specimens from one locality.

Head.—Seen from above very broad, with a sharp lateral angle at the base of the mandible; the longest seta in front of this angle about as long as the breadth of the basal antennal joint. The central rod without visible frontal branches; posteriorly it is scarcely visible, or generally terminating at a rather long distance from the hind margin of the head, and a posterior area and oblique posterior rods are not seen.

Antennæ.—The number of joints is generally from thirty to thirty-four (in one specimen one antenna has twenty-one joints, the other is broken.) The setæ on the inner side of the proximal joints not longer than those on the outer side. The secondary whorl begins on the lower side about on the eighth joint; on more than the distal half of the antenna this whorl is well developed on the ventral half of the joints (fig. 2*a*), and besides one seta, sometimes two setæ are found above on the same joints; on one or two joints just behind the terminal one a seta is often found below, behind the secondary

whorl. The setæ in the central whorl of nearly all joints are long, slightly shorter below than above. The terminal joint (fig. 2 *b*) with a large and long-stalked striped organ inserted on a conspicuous protuberance, and besides a small and very short-stalked similar organ.

Scuta.—The second scutum (fig. 2 *d*) with the posterior margin slightly convex; its antero-lateral setæ considerably longer than the breadth of the proximal antennal joints, and directed at least a little forwards; two pairs of lateral setæ are longer than the others, but scarcely more than half as long as the antero-lateral setæ, and directed essentially backwards. The first, third, fifth, sixth, and eighth scuta, each with the antero-lateral setæ and two pairs of lateral setæ about of the same length and direction as the corresponding setæ on the second scutum; a long and outward-directed pair of antero-lateral setæ are wanting in the fourth, seventh, and ninth, and following scuta, while they possess a pair of rather long lateral or postero-lateral setæ directed backwards. The penultimate scutum is posteriorly conspicuously emarginate, with broadly rounded lobes (fig. 2 *e*).

Legs.—The last pair (fig. 2 *f*) with the tarsus slender, nearly five times longer than deep; the metatarsus with five or six, the tarsus with seven setæ in the anterior dorsal row; the setæ gradually increase somewhat in length on each of these joints from the base towards the end, and the longest of them, the distal seta on the metatarsus, is about half as long as the depth of the metatarsus; none of the joints with any rather long seta. The anterior claw (fig. 2 *g*) is very long, originating from the circumstance that its distal more slender part is strongly elongate; it is, besides, moderately curved, while the other claw is considerably curved, very slender, but only three fifths as long as the anterior one; the front seta is rather weak. The exopod is slightly shorter than the depth of the metatarsus. The first pair of legs (fig. 2 *h*) with the anterior claw elongate, slender, and somewhat curved (fig. 2 *i*); the other claw is very slender, short, at most scarcely reaching the middle of the long claw, and often

terminating at some distance before this point; the front seta is as long as the short claw, and very robust.

Cerci (fig. 2 *k*).—In larger specimens from a little more than four and a half to five times longer than deep. They are clothed with a large number of stiff, rather short setæ, nearly equal in length at the end and before the middle, and none of them half as long as the depth of the cerci. The terminal area looks upwards, and generally a little outwards; it is a little longer than the setæ. The apical seta is strong, as long as or somewhat longer than the depth of the cerci.

Length.—3 to 3.6 mm.

Locality.—La Moka, in Venezuela, August 1st, 1891 (F. Meinert).

Remarks.—This species is distinguished from all other forms by the very elongate anterior claw on the posterior pairs of legs. Other useful features have been pointed out in the analytical key.

4. *Scutigera caldaria*, n. sp. Pl. 2, figs. 3 *a*—3 *g*.

Material.—Many specimens from hothouses. Some South American specimens probably belonging to this species are dealt with in the "Appendix" to the description.

Head.—Seen from above it is proportionately a little narrower, and its lateral angles a little less pronounced than in *S. unguiculata*; the longest lateral seta is considerably shorter than the breadth of the proximal antennal joints. The central rod without visible frontal branches or posterior rods as in *S. unguiculata*.

Antennæ.—The number varies generally from twenty-three to twenty-eight. The setæ on the inner side of the proximal whorls not longer than those on the outer side. The secondary whorl begins on the lower side on the seventh or eighth joint, but already at the middle of the antennæ it is completely developed above and on the outer side. On the same distal half at least one seta, often two setæ, are found on the lower side, behind the second whorl (fig. 3 *a*), and the most distal joints have even four setæ behind each other on

the lower margin. The setæ in all whorls at least somewhat shorter than in *S. unguiculata*, and especially the setæ on the lower half of the joints considerably shorter than in that species. The terminal joint with one large and long-stalked striped organ on a rather low protuberance, and besides a small and very short-stalked similar organ.

Scuta (fig. 3*b*).—As to shape and arrangement and number of setæ they do not differ perceptibly from those in *S. unguiculata*, but the antero-lateral setæ are slightly shorter.

Legs.—The last pair (fig. 3*c*) is more slender than in *S. unguiculata*, and the tarsus is five times longer than deep. The metatarsus with five or six, the tarsus with seven spines in the outer dorsal row; the setæ increase gradually a little in length from the base to the end of each joint, but the longest setæ are decidedly shorter than half the depth of the metatarsus; the dorsal setæ on the tibia are short. The anterior claw (fig. 3*d*) curved as in *S. unguiculata*, but less slender and considerably shorter than in that species; the posterior claw is of moderate depth, rather curved, and two thirds as long as the other; the front seta rather short. The exopod long, a little shorter than the depth of the metatarsus. The first pair of legs with the anterior claw (fig. 3*e*) elongate, moderately slender, and a little curved; the other is moderately slender, and a little more than half as long as the anterior one. The front seta is shorter than the short claw and moderately robust; not very conspicuous.

Cerci (fig. 3*f*).—Nearly as in *S. unguiculata* both as to shape and clothing, only a little shorter and thicker, being slightly more than four times longer than deep, and the clothing of rather short setæ a little more dense. The terminal area looks upwards.

Length.—2·8 to 4 mm.

Locality.—In the tan-bark in hothouses in the royal garden, "Rosenborg Have," Copenhagen, I discovered this species many years ago, and have found it again every time I visited the place. I have also found it in similar bark in a very warm hothouse in the Botanical Garden in Copenhagen.

Furthermore, I have examined four specimens captured in hothouses of the Museum in Paris.

Remarks.—This species is closely allied to *S. unguiculata*, but differs by the claws on the posterior legs, the posterior claw on the first pair of legs, besides by more numerous and shorter setæ on the distal half of the antennæ, etc.

Appendix.—From three localities in the southern half of South America I have seen four specimens which probably belong to this species. Three of these specimens have acquired the full number of legs, and measure from 2·6 to 3·2 mm.; only one of their antennæ has been completely preserved, and it contains nineteen joints. They agree essentially with *S. caldaria*, and the differences observed are small. The setæ on the antennal joints are a little longer than in *S. caldaria*, but as to the other features mentioned above quite similar; the last pair of legs with the tarsus a little less slender, four and a half to four times longer than deep, with seven or six dorsal setæ in the anterior row, its anterior claw slightly shorter than in the form from the hothouses. I am inclined to consider these South American specimens as belonging to the original form, from which the specimens in the European hothouses have descended; but my American material is scanty, only moderately preserved, and the specimens perhaps not quite full-grown, wherefore I do not venture to decide the question with absolute certainty. The American specimens have been collected by Dr. Silvestri in the following localities:—Guayaquil in Ecuador; Cuyabà, in the province Matto Grosso, Southern Brazils; and Paraguairi in Paraguay.

5. *Scutigera orientalis*, n. sp. Pl. 2, figs. 4a—4g;
Pl. 3, figs. 1a—1f.

Material.—Many specimens from several localities.

Head.—Seen from above (fig. 1a) it is very broad, with a well-developed lateral angle; the longest seta in front of

this angle is slightly longer than the other setæ, and considerably or much shorter than the breadth of the proximal antennal joints. The central rod is scarcely visible in more than half of the normal length, without frontal branches, and terminating behind rather far from the posterior margin, without visible oblique posterior rods or posterior area.

Antennæ.—The number of joints varies essentially, according to the length of the specimens, from twenty-two to forty-one. The setæ on the inner side of the proximal joints are as long as or slightly longer than those on the exterior side (fig. 1 *b*). The second whorl begins below near the end of the basal third of the antennæ; a little more distant from the base it has a seta on the upper side, but the whorl is only completely developed on the outer side in the most distal joints in large specimens. About the middle of the antennæ (fig. 1 *c*) a third whorl begins on the lower side, but it contains only one seta, and towards the end of the antennæ two or three setæ. The setæ in the central whorl are long on the upper and only a little or scarcely shorter on the lower side. The terminal joint has a large, long-stalked, striped organ on a conspicuous protuberance, two small, very short-stalked striped organs, besides a subglobular organ without stalk and stripes and some styliform, small sensory setæ.

Scuta.—The second scutum (fig. 1 *d*) has its posterior margin straight or slightly convex in the middle half; its antero-lateral setæ are directed somewhat forwards, long, somewhat longer than or nearly twice as long as the breadth of the basal antennal joints; of its lateral setæ two pairs are longer than the other, and the postero-lateral pair, being the longest, is only half as long as the antero-lateral pair, and directed essentially backwards. The first, third, fifth, sixth, and eighth scuta each with an antero-lateral seta about as long as that on the second scutum (in one specimen these setæ on the sixth and eighth scuta were considerably shorter than the anterior ones), and one pair or two pairs of lateral setæ developed as on the second scutum; the fourth,

seventh, and ninth to thirteenth scuta without any long and protruding antero-lateral seta, but with one pair or two pairs of lateral setæ as long as those on the second scutum and directed essentially backwards. The penultimate scutum posteriorly a little emarginate (fig. 1 *e*).

Legs.—The last pair (figs. 4 *a* and 4 *e*) with the tarsus four and a half to five times longer than deep; the metatarsus with five to six, the tarsus with seven to eight setæ in the anterior dorsal row; these setæ and the distal dorsal setæ on the tibia differ but little in length, and the longest one of them is not half as long, generally only one third as long, as the depth of the metatarsus. The anterior claw (figs. 4 *b* and 4 *f*) of moderate length, or even rather short, rather robust; the posterior claw is somewhat more slender, considerably more curved, and somewhat or considerably shorter than the other; the front seta is moderately long and robust. The exopod is of moderate length, about two thirds as long as the depth of the metatarsus. The first pair of legs (fig. 4 *c*) with the anterior claw (figs. 4 *d* and 4 *g*) rather long and feebly curved; the other is small, at most scarcely half as long as the anterior one, and often considerably shorter; the front seta almost claw-like, exceedingly thick, and as long as or a little longer than the short claw.

Cerci (fig. 1 *f*).—From slightly more than four times (in small specimens) to nearly five times longer than deep, set with a large number of rather short setæ; the distal setæ are slightly or scarcely longer than those at the middle, none of them half as long as the depth of the cerci, and often slightly more than one third of this dimension. The terminal area looks upwards and a little outwards, and is longer than the lateral setæ. The apical seta is as long as or somewhat longer than the depth of the cerci.

Length.—Specimens with the full number of legs vary from 2.3 to 5 mm.

Locality.—Sumatra and Java, where it has been captured by Prof. Max Weber in various localities: Singkarak and Mount Singalang (both in Sumatra), and Tjibodas

(Java). (R. I. Pocock has determined these specimens as *S. immaculata*, and published the result and the localities in the paper mentioned above on p. 33.) Furthermore, the species has been captured on the island of Koh Chang (Gulf of Siam) by Dr. Th. Mortensen; under stones, January 7th, 12th, 15th, 1900; under plants on stones, January 6th, 1900; under an old stem of a tree, March 14th, 1900; in the wood at the river Klong Salakpet, March 15th, 1900,—in all thirty-nine specimens. Finally, five specimens from Bangkok in the Brit. Mus. were collected by Capt. S. S. Flower.

Remarks.—This species is rather closely allied to *S. caldaria*, but differs by several small characters; the setæ on the distal half of the antennæ are less numerous, but especially those in the central whorl are a good deal longer, the penultimate scutum less emarginate, the claws on the posterior legs a little shorter and more robust, the first pair of legs with the posterior claw shorter, and the front seta considerably more robust.

6. *Scutigera plebeia*, n. sp. Pl. 3, figs. 2 *a*—2 *d*.

Material.—One badly-preserved specimen with some appendages, and many setæ broken off.

Head.—Moderately broad with a conspicuous lateral angle; the longest seta in front of the angle seems to be lost,—if not, it is only half as long as the breadth of the proximal antennal joints. The central rod without visible frontal branches, and terminating behind in a very faint triangular area, which touches the posterior margin of the head.

Antennæ.—The major part of both antennæ is lost; of the one thirteen, of the other eleven joints have been preserved. These joints are simple, and their setæ in the central whorls are rather short. The secondary whorl begins below on the ninth joint.

Scuta.—The second scutum with the posterior margin slightly convex near the middle; the antero-lateral setæ

have been broken off, but their insertions are very distinct. In the first scutum one of these projecting setæ has been preserved; it is somewhat longer than the breadth of the proximal antennal joints, and the corresponding setæ on the second scutum were certainly at least as long. Most of the other marginal setæ on the second scutum are also wanting, but judging from their small areas of insertion none of them were more than moderately developed. On the third, fifth, sixth, and eighth scuta the large insertions of the antero-lateral setæ are plainly seen; in the other scuta they are wanting, as in *S. orientalis*, etc. The penultimate scutum is posteriorly somewhat emarginate, nearly angularly concave in the median line.

Legs.—The last pair and the left leg of the eleventh pair are wanting; the right leg of the eleventh pair differs scarcely from the tenth pair, of which the left leg has been drawn (fig. 2 *a*), and is described here. The tarsus is four and a half times longer than deep. The metatarsus with four, the tarsus with five setæ in the anterior dorsal row; these setæ differ but little in length from each other, and none of them are quite half as long as the breadth of the metatarsus; the most distal dorsal seta on the tibia is slightly longer than those on the metatarsus. The anterior claw (fig. 2 *b*) is medium sized, rather curved, and distally somewhat elongate; the posterior claw is slender, considerably curved, and only three fifths as long as the other; a front seta is not conspicuous. The exopod is scarcely two thirds as long as the depth of the metatarsus. The first pair of legs with the anterior claw (fig. 2 *c*) very long and somewhat curved; the posterior claw is short, not reaching the middle of the other; the seta not longer than the short claw, and moderately slender.

Cerci (fig. 2 *d*).—A little more than four times longer than deep, set with a rather good number of stiff setæ, gradually increasing considerably in length from the base outwards, and the most distal ones are about two thirds as long as the depth of the cerci. The terminal area about as

long as the distal setæ, and looks upwards; the apical seta is wanting in my specimen.

Length.—The specimen measures 3·6 mm.

Locality.—Island Mauritius, "Curepipe." The specimen has been captured by Mr. Chr. Alluaud, and belongs to the Museum in Paris.

Remarks.—The species is allied to *S. orientalis*, but is easily distinguished from this and other species described above by the cerci, the setæ of which are less numerous, but the distal ones of them conspicuously longer and stronger than in those species.

7. *Scutigera nivea* (Scopoli). Pl. 3, figs. 3*a*—3*h*.

1763. *Scolopendra nivea*, Scopoli, 'Entomologia Carniolica,' Vindebonæ, p. 416.

1884. *Scolopendrella nivea*, Latzel, 'Die Myriop. d. öster.-ungar. Monarchie,' ii, p. 14, 'Taf. i, fig. 1.

1885. *S. nivea*, Berlese, 'Acari, Myriopoda, et Scorpiones hucusque in Italia rep.,' fasc. xxiii, No. 4.

1886. *S. nivea*, Grassi, 'Mem. d. Reale Accad. d. Sci. di Torino,' Ser. 2^a, t. xxxvii, p. 594.

(In this list papers by Karlinski and Tömösváry have been omitted as unknown to me, and certainly unimportant; they have been mentioned by Latzel, op. cit., pp. 14 and 15. *Scolopendrella gratiæ*, Ryder, is uncertain, and has therefore not been included in the list.)

Material.—Five specimens, all small and shrivelled or incomplete. The following description is therefore rather defective.

Head.—Moderately broad, with the lateral margin angular. The longest seta in front of the angle is considerably shorter than the breadth of the basal antennal joint. The central rod is conspicuous in its whole length; at the front end of the basal third it seems to be divided by a transverse suture; the posterior part widens somewhat near the hind margin of

the head, and from its anterior angles just behind the suture a thin branch proceeds obliquely forwards and outwards; the frontal branches of the central rod are faint.

Antennæ.—The highest number of joints observed by me is twenty-one; Latzel states that it varies from twenty to thirty. The proximal joints are scarcely thickened, but the setæ on their inner surface seem to be somewhat longer than the others, which are rather short. A special description cannot be attempted, as the preservation is too bad. The terminal joint has a rather small striped organ with short stalk, and at least one still smaller organ of the same kind besides.

Scuta.—The second scutum (fig. 3 *a*) with the posterior margin straight or very slightly emarginate in the middle portion; the antero-lateral setæ are directed somewhat forwards, very long, much longer than the breadth of the proximal antennal joints; a lateral seta is slightly more than half as long as the antero-lateral one, and directed essentially backwards; a postero-lateral seta and some of the posterior setæ are of moderate length. The first, third, fifth, sixth, eighth, ninth, eleventh, and twelfth scuta each with a pair of setæ directed essentially outwards, and about as long as the antero-lateral setæ on the second scutum; on the anterior ones of these scuta these setæ are antero-lateral, on the posterior scuta they are inserted more backwards, but always on the most lateral point of the scuta; besides, a lateral seta of moderate length is found on several of the scuta. The thirteenth scutum (fig. 3 *b*) is posteriorly slightly emarginate, and a long seta directed more or less backwards is inserted at the posterior end of the lateral margin.

Legs.—The last pair of my small specimens have the tarsus four times longer than deep (fig. 3 *c*), and not widened towards the base; the tibia has two dorsal setæ, one of which is very long, the metatarsus with two similar setæ in the anterior dorsal row, and these setæ are only a little shorter than the depth of the metatarsus; the tarsus in the anterior dorsal row with three setæ, which are a little shorter and

thinner than those on the metatarsus. The claws (in my small specimens) are rather short, and not very different in length (figs. 3*d* and 3*e*); the front seta is moderately developed. The exopod is somewhat shorter than the depth of the metatarsus. The first pair of legs with the claws moderately developed in all respects (figs. 3*f* and 3*g*), the anterior one much—but not twice—longer than the other; the front seta is long and slender.

Cerci (fig. 3*h*).—They are proportionately small, and from scarcely four to four and a half times longer than deep, with the distal part produced and curved upwards; they are set with comparatively very few setæ, which increase very much in length from the base of the cerci outwards, and the most distal setæ are from a little to considerably longer than the depth of the cerci; a proportionately long distal portion of the cerci without any setæ. The terminal area is rather long and looks outwards, sometimes somewhat upwards as well. The apical seta is exceedingly long, much longer than the depth of the cerci.

Length.—The adult specimens seen by me measure 1.7 to 2 mm.; according to Latzel the length varies from 2 to 5 mm.

Locality.—Palmi in Calabria, one specimen (the author); four specimens have been captured by Mr. C. Börner either near Palmi or at Catania (Sicily).

Distribution.—Latzel has examined specimens from various parts of Austria-Hungary and from Russian Poland; Muhr records the species from Bohemia. As mentioned above on p. 43, it remains doubtful whether *S. gratiæ*, Ryder, captured at Philadelphia, near Washington, D.C., and in two other localities in the United States, is synonymous with *S. nivea*, Scop., or belongs to a closely allied species.

Remarks.—This species is easily distinguished from all forms described above by having outstanding long setæ on the ninth, eleventh, and twelfth scuta, and by having comparatively very few setæ but some of them very long on the short cerci. From the two following species it is sharply

distinguished by having only one pair of very long and somewhat forwardly-directed setæ on the second scutum.

8. *Scutigereilla chilensis*, n. sp. Pl. 3, figs. 4 *a*—4 *g*.

Material.—Several specimens from two localities, but all with at least many of the long setæ broken off.

Head.—It is short and very broad, with a very pronounced lateral angle; the longest lateral seta, situated somewhat in front of the angle, is very long, much longer than the breadth of the basal antennal joint. The visible part of the central rod is rather long, and somewhat before the hind margin of the head is connected with the vertex of a large triangle, the sides of which are rather feebly developed oblique rods; the frontal branches could not be observed.

Antennæ.—The number of joints varies from thirty to forty. A rather small number of proximal joints with one or two setæ on the inner side directed much forward and somewhat longer than those on the outer side. The secondary whorl begins below on about the tenth joint, on the upper side on the fifteenth joint, and from this joint begins besides a third whorl on the lower side. The setæ in the central whorl are rather long on the upper and a little shorter on the lower side. The terminal joint is elongate, with a rather large, long-stalked, striped organ placed on a broad protuberance, besides which there are two small organs of the same kind, and some styliform, somewhat sinuate sensory setæ.

Scuta.—The second scutum (fig. 4 *a*) with the posterior margin flatly convex; the antero-lateral setæ are exceedingly long, more than twice as long as the proximal antennal joints; another seta inserted a little more behind is as long as or even a little longer than the antero-lateral one, and directed outwards and forwards; a pair of setæ on the hind margin is two thirds as long as the lateral pair mentioned, and some other setæ are moderately long. The first scutum is adorned with two pairs of setæ nearly as long as the second one; the third scutum only with one pair of long

setæ, but they are even longer than the antero-lateral setæ on the second scutum; on the following scuta most of the characteristic setæ have been lost, so that it is impossible to produce a description. The penultimate scutum (fig. 4 *b*) has the posterior margin very slightly convex to very slightly emarginate at the middle; the figure shows that it is adorned with some pairs of longish or long setæ, but the posterior lateral pair, which probably are the longest of them all, have been broken off, and are therefore indicated in the figure with dotted lines.

Legs.—The last pair (fig. 4 *c*) with the tarsus almost four times longer than deep, and scarcely widened towards the base. The tibia with a distal dorsal seta, which is very strong, and nearly as long as the depth of the joint; the metatarsus with four setæ in the anterior dorsal row, of which the distal ones are two thirds as long as the depth of the joint; furthermore, behind the distal dorsal seta there is another seta as long as or longer than the depth of the metatarsus; the tarsus with five setæ in the anterior dorsal row, partly as long as or a little longer than the depth of the joint. The anterior claw (fig. 4 *d*) is moderately long, rather robust, and somewhat curved; the posterior claw is somewhat shorter than the other, less robust, and much more curved; the front seta is long and slender. The exopod two thirds as long as the depth of the metatarsus. The first pair of legs (fig. 4 *e*) with the anterior claw (fig. 4 *f*) long, slender, and somewhat curved; the posterior claw nearly two thirds as long as, but somewhat more slender and a little more curved than the other; the front seta moderately long and moderately robust.

Cerci (fig. 4 *g*).—They are from a little more than four and a half to five times longer than deep, set with a moderate number of strong setæ, which increase gradually but considerably in length from the base outwards, and the distal ones are a little longer than the depth of the cerci; the distal part of the cerci is more or less produced and without setæ. The terminal area looks upwards, and is of medium length or rather long. The apical seta has been lost in my specimens.

Length.—4 to 5 mm.

Locality.—Chile: S. Vicente, April 9th, 1899, nine specimens; Temuco, April 4th, 1899, five specimens (F. Silvestri, coll.).

Remarks.—This species is sharply distinguished from all other forms, with exception of *S. capensis*, by its second scutum, which has two pairs of very long setæ directed outwards and forwards, and the posterior angles flatly rounded and not produced; from *S. capensis* it is easily separated by the long setæ on the metatarsus and tarsus of the posterior legs, by the shape of the claws, by its cerci being comparatively thicker, etc.

9. *Scutigera capensis*, n. sp. Pl. 3, figs. 5 *a*—5 *f*;
Pl. 4, figs. 1 *a*—1 *e*.

Material.—Three specimens, not very well preserved. One specimen is large and adult, another is somewhat smaller, with only eleven pairs of legs, and both have been taken in the same locality. The third specimen, captured in another place, has the full number of legs, but is nevertheless much smaller than the specimen with eleven pairs of legs; it presents besides several minor differences from the two large specimens. I have therefore found it practical to base the following description of this species on the two large specimens, especially on the adult one, and to deal with the third specimen under "variation."

Head.—It is short and very broad, with well-developed lateral angle, and the longest seta in front of this angle is a little longer than the breadth of the proximal antennal joints. The state of preservation did not allow a study of the central rod.

Antennæ.—They are incomplete, but in the adult specimen thirty-seven joints have been preserved in one of them. The whorls (fig. 1 *a*) agree much with those in *S. chilensis*, with the exceptions that the secondary whorl does not begin on the upper side before about the twentieth joint, that the

setæ in the central whorl are a little shorter, and that even some setæ belonging to a fourth whorl are present on the lower side of a comparatively long distal part of the antennæ.

Scuta.—The second scutum (fig. 1 *b*) with the posterior margin very flatly convex; the antero-lateral setæ are turned much forward and somewhat longer than the breadth of the proximal antennal joints. A little more posteriorly a lateral seta is inserted, which is considerably longer than the antero-lateral one, and directed outwards and somewhat forwards. Most of the setæ along the posterior margin are proportionately rather long, and one pair, which are inserted a little farther from the margin, are conspicuously longer than the antero-lateral pair. On the first scutum the antero-lateral pair are not half as long as the lateral pair, which are very long, and a pair inserted at some distance from the posterior margin are only a little shorter than the lateral pair. All following scuta, from the third to the thirteenth, each with at least one pair of lateral long setæ; on the third, fifth, eighth, and eleventh scuta a pair of antero-lateral setæ could be observed, but all incomplete or broken off. The penultimate scutum (fig. 1 *c*) a little emarginate in the middle of the hind margin, with two pairs of setæ slightly shorter than the long lateral pair.

Legs.—In the adult specimen the last pair of legs (fig. 5 *a*) are rather long; the tibia on the dorsal side, with some short setæ and a distal, very thick seta, which is two thirds as long as the depth of the joint; the metatarsus nearly twice as long as deep, with six short setæ in the anterior dorsal row; the tarsus is strongly widened towards the base, three times longer than deep, with eight rather short setæ in the anterior dorsal row; the anterior claw (fig. 5 *b*) is short, with the basal part deep; the posterior claw is proportionately slender, much curved, and more than two thirds as long as the other; the front seta is very long and robust. The tenth pair (fig. 5 *c*) somewhat shorter, and especially with the two distal joints much more slender than in the twelfth pair, the metatarsus being two and a half times, the tarsus more than four

and a half times longer than deep; the distal dorsal seta on the tibia is moderately short; the posterior claw (fig. 5*d*) very slender, and considerably shorter than the thick anterior claw, the front seta longer than the anterior claw, and proximally exceedingly robust. (The penultimate pair show a transition stage between the two pairs described.) The first pair of legs (fig. 5*e*) with a few long or very long setae on the lower side of the femur; the tarsus with the distal setae unusually long, the anterior claw (fig. 5*f*) proportionately not slender and feebly curved, the posterior claw scarcely half as long as the other, slender and moderately curved, the front seta long and very robust. (In the specimen with eleven pairs of legs the last pair resembles the tenth one in the adult described.)

Cerci (fig. 1*d*).—Of moderate length, but unusually slender, nearly six times longer than deep. They are set with a moderate number of setae, which increase somewhat in length from the base outwards, and the most distal setae are a little shorter or a little longer than the depth of the cerci. The terminal area looks upwards, and more or less outwards as well; it is rather short. The apical seta is wanting in my specimens.

Length.—The adult and rather contracted specimen is 4.7 mm.

Variation.—A specimen which measures scarcely 3 mm. in length, but possesses the full number of legs, presents some differences from the form just described. On the two anterior scuta the antero-lateral setae are a good deal shorter, but the long lateral pair are somewhat longer than in the specimen figured. The last pair of legs with the distal dorsal spine on the tibia about as long as the depth of the joint; the tarsus is slender, nearly five times longer than deep, with seven dorsal setae, the anterior somewhat longer and conspicuously less robust than in the main form; the cerci (fig. 1*e*) are a little more than five times longer than deep, with the setae less numerous and conspicuously longer in proportion to the cerci; the terminal area is proportionately longer

and looks upwards, the apical seta as long as the longest lateral one. In my opinion this small specimen belongs, nevertheless, to the same species as the large form described above; but, my material being too scanty for a really complete characterisation of the species, I have preferred to mention the small specimen separately instead of admitting its features in the description itself.

Locality.—All three specimens have been captured in August, 1894, by Prof. Max Weber in the Cape Colony, the two large specimens at Table Bay and the small one at Constantie, near Cape Town.

Remarks.—This species is rather allied to *S. chilensis*; the reader is referred to the "Remarks" on that species.

10. *ScutigereUa angulosa*, n. sp. Pl. 4, figs. 2 *a*—2 *k*
(and var. figs. 3 *a*—3 *h*).

Material.—Nine specimens from four localities rather distant from each other, and five of them with the full number of legs. Two other specimens from a fifth locality differ in several features, and they have therefore not been taken into consideration in the description of the species, but are dealt with under "Variation."

Head.—Seen from above it is moderately narrow in proportion to the length; the lateral margin is a little angular or rather flatly rounded; the long seta is inserted somewhat in front of the posterior end of the mandible, and is at least as long as the breadth of the basal antennal joint. The central rod is rather long, without visible frontal branches; posteriorly it is connected with the vertex of a rather large triangle at the hind margin, and the sides of this triangle are oblique rods, which are moderately developed in nearly their whole length.

Antennæ.—In the adults the number of joints varies from twenty-four to twenty-seven. Some few proximal joints (fig. 2 *a*) on the inner side with one or two thin setæ directed much forward and somewhat longer than those on

the outer side. The second whorl begins below on the fifth to seventh joints, and above on the seventh or eighth; at the middle of the antennæ not only is this whorl complete, but a seta is inserted below between the two whorls, and on the distal joints three setæ are well developed behind each other on the lower margin. The setæ in the central whorls are scarcely of medium length, slightly longer above than below. The oblong terminal joint has (fig. 2 *b*) a moderately large or large and long-stalked striped organ inserted on a protuberance, a rather small and short-stalked organ with feebly developed stripes, and some styliform, slightly curved sensory setæ.

Scuta.—The second scutum (fig. 2 *c*) with the posterior margin rather deeply emarginate; the lobes on each side of this emargination are posteriorly angular, thus forming a kind of triangular plate which is several times broader than long; the antero-lateral setæ are directed somewhat forwards and considerably longer than the breadth of the basal antennal joint; a lateral pair of setæ are directed essentially outwards, and are as long as or longer than the antero-lateral pair; at each posterior angle a rather long seta is inserted. The scuta, the last one excepted, posteriorly emarginate, and with two angles essentially as in the second scutum; the first, fifth, eighth, eleventh, and thirteenth scuta each with an antero-lateral and a lateral pair of setæ (on the thirteenth scutum [fig. 2 *d*] these are lateral and postero-lateral) partly somewhat longer and partly somewhat shorter than the corresponding two long pairs on the second scutum, and all directed at least much outwards (with exception of the posterior pair on the penultimate scutum); the third, fourth, sixth, seventh, ninth, tenth, and twelfth scuta each with one pair of long or very long protruding setæ; all scuta with a pair of rather long or long setæ inserted at the posterior angles and directed upwards, and these last setæ are present even on the last scutum on each side of a median shallow depression.

Legs.—The posterior pairs present considerable variation

in various respects. In the largest specimen the last pair (fig. 2 *e*) is exceedingly thick, the metatarsus being only one half longer than deep, and the tarsus, which is strongly widened towards the base, slightly more than three times longer than deep; the tibia has on the upper side some short setæ, and a distal, very thick seta which is slightly shorter than the depth of the metatarsus; the metatarsus with four dorsal setæ, the second of which is rather long, longer than the first and the third, while the fourth is only a little shorter than the long seta on the tibia; the tarsus with five dorsal setæ, the first and the fifth short, the three others rather long. In another adult specimen the twelfth pair (fig. 2 *g*) is considerably more slender, the metatarsus being twice as long as deep, and the tarsus almost four times longer than deep; the distal seta on the tibia is somewhat shorter, the metatarsus with four dorsal setæ, and three of these as in the large specimen, while the fourth is even somewhat longer than the depth of the joint; the tarsus with four setæ, the second and third rather long. In the large specimen the ninth pair of legs are about as robust as the twelfth pair of the other specimen, and the tenth and eleventh pairs form transition stages to the thick twelfth pair described above. (In a small and immature specimen with eleven pairs of legs the eleventh pair [fig. 2 *k*] are rather aberrant, the metatarsus being only one third longer than deep, and the tarsus, which is slender at the end, is proximally very broad, and so deep that it is not three times longer than deep; the setæ can be seen on the figure. The posterior pairs of legs decrease gradually in thickness from behind forward, so that the eighth pair are slender. It can be asserted that the specimen does not present any other difference from the typical form.) The anterior claw (fig. 2 *f*) of the last pair of legs always of medium length, moderately robust and somewhat curved; the posterior claw is a little more slender, and about two thirds as long as the other; the front seta is rather long, but proportionately slender. The exopods are rather long. The first pair of

legs with the anterior claw (fig. 2 *h*) moderately long and rather curved; the posterior claw is between half and two thirds as long as the other; the front seta as in the last pair of legs.

Cerci (fig. 2 *i*).—From a little more than four to five times longer than deep, with the distal part somewhat elongate. They are set with a very moderate number of stiff setæ, which increase gradually but considerably in length outwards, and the distal ones are about as long as the depth of the cerci; a moderately long distal part is without setæ. The terminal area looks upwards or a little outwards as well, and is moderately long. The apical seta as long as one of the distal lateral setæ.

Length.—2.4 to 4.5 mm.

Variation.—A very considerable variation in the shape and adornment of the posterior pairs of legs has been described above. But two specimens which I, after some hesitation, have referred to this species have not been taken into account in the description above; I have preferred to mention them separately here as *Scut. angulosa*, var. *brevicornis*, var. *nova*. Both specimens have been captured in one locality, and they are very similar to each other in all respects. They possess the full number of legs, and one of them measures 3.2 mm. in length, while the other is a little shorter. I will only describe the differences between this variety and the specimens taken as typical. The antennæ contain fifteen and sixteen joints; the secondary whorl (fig. 3 *a*) begins both below and above on the fifth joint; the terminal joint differs as to the sense-organs; on the part visible from the exterior side (fig. 3 *b*) it has a pair of styliform setæ, a rather large subglobular organ without stripes, and three striped organs, the largest of which is rather small with a moderately long stalk, while the others are short-stalked. The long setæ on the scuta (figs. 3 *c* and 3 *d*) a little shorter than in the typical specimens. The last pair of legs (fig. 3 *e*) shaped about as in smaller specimens of the typical form, but presenting some differences in the setæ

and claws; the distal seta on the tibia as long as the depth of the metatarsus; this last joint with three dorsal setæ, and the distal one of these somewhat longer than the others, but only a little more than half as long as the depth of the joint; the tarsus with four dorsal setæ in the anterior row; the anterior claw (fig. 3 *f*) is rather short and robust, rather curved, and only a little longer than the posterior claw, which is somewhat more slender but scarcely more curved than the other. The first pair of legs with the anterior claw (fig. 3 *g*) rather short and robust, the posterior claw much more slender and nearly two thirds as long as the other, and both claws are moderately curved. The cerci (fig. 3 *h*) slightly more than three and a half times longer than deep, and the setæ somewhat more numerous than in the typical form. The experience as to the degree and quality of the variation of *Scut. immaculata* (Newp.) in Europe has taught me that the animals described here must be considered as a variety of *Scut. angulosa*, the most essential differences between the typical form and the variety being the claws on the posterior legs and the sense-organs on the terminal joint of the antennæ.

Locality.—The southern third of South America, in various localities: Monte Buenos Aires, in Gobern, S. Cruz, southern Patagonia, five specimens, among which are the largest specimens examined; Porto Piramides, Chubut, Patagonia, the two specimens described as the variety *brevicornis*; S. Pedro, Misiones, Argentina, a typical specimen with the full number of legs, but measuring only 2.4 mm. in length; Posadas, Misiones, Argentina, the immature specimen of which the posterior pair of legs have been mentioned above and shown in fig. 2 *k*; Salto, in Uruguay, two small, immature specimens. All specimens have been captured by Dr. F. Silvestri.

Remarks.—The species is easily recognised from all other forms of the genus by the shape of the second scutum, together with the number and length of its outwards-directed setæ and the well-developed exopods at the posterior legs.

GROUP III.

11. *Scutigera crassicornis*, n. sp. Pl. 4, figs. 4*a*—4*c*;
Pl. 5, figs. 1*a*—1*g*.

Material.—Eight well-preserved specimens, five of which are adult.

Head.—Seen from above (fig. 1*a*) it is moderately narrow, scarcely angular on the sides, and the usual lateral seta is as long as the basal antennal joint. The central rod is not visible anteriorly, terminating apparently in front of the middle in rudiments of two branches; posteriorly it is connected with the vertex of a triangle situated at the hind margin of the head; the sides of this triangle are concave, consisting of rather feeble oblique rods.

Antennæ.—The number of joints varies from twenty-seven to thirty-one. In one case twenty-one joints have been observed in an animal with twelve pairs of legs. The joints from the second to the ninth or tenth (fig. 4*a*), and especially the fifth to the eighth, are considerably thickened in the adults—to a less degree in immature specimens,—and on the inner side (fig. 4*b*) two or three of the setæ in the central whorl are strongly elongate, the longest three to four times longer than the outer setæ, and nearly vertical on the longitudinal axis of the antennæ. The second whorl begins below on the eighth to the tenth joint, but is quite absent on the upper side of all joints (fig. 1*b*). The joints, with exception of seven or eight proximal ones, have a small, conical, robust rod on the upper side in front of the central whorl. The terminal joint with a rather large and long-stalked striped organ inserted on a lower protuberance, one or two small and short-stalked striped organs, and finally a large wart-like protuberance, on which I have never found any organ.

Scuta.—The second scutum (fig. 1*c*) with the posterior

margin deeply emarginate, the emargination angular in the middle and limited by lobes, which are broadly rounded or a little angular at the hindmost point. The antero-lateral setæ are directed outwards, and nearly as long as the breadth of the first antennal joint. A lateral seta inserted considerably more behind is a good deal shorter, though very conspicuous. All the other marginal setæ are short. The first, third, fifth, sixth, eighth, and ninth scuta each with an antero-lateral seta from slightly longer to somewhat shorter than those on the second scutum, but the seta is often directed considerably backwards on the more posterior of these segments. The penultimate scutum posteriorly deeply emarginate, with the lobes somewhat angular behind. The last scutum posteriorly with a moderately large, median, deep depression, which is a little longer than broad; no overlapped cavity has been developed.

Legs.—The last pair (fig. 1 *d*) with the tarsus four times longer than deep. The metatarsus with five and the tarsus with seven setæ in the anterior dorsal row; on each joint these setæ increase gradually somewhat in length towards the end, but the longest setæ on both joints are not half as long as the depth of the metatarsus; a seta of similar length is found near the end of the upper side of the tibia. The anterior claw (fig. 1 *e*) is moderately long, proximally rather robust; the posterior claw is rather slender, strongly curved, and a little to somewhat shorter than the other; the front seta scarcely of middle length and not robust. The exopod is short, considerably shorter than the depth of the tarsus. The first pair of legs (fig. 1 *f*) with the claws (fig. 1 *g*) subequal in shape, the posterior one slightly shorter than the other, the front seta short and thin.

Cerci (fig. 4 *c*).—Not quite four times longer than deep, with the distal part somewhat elongate. They are clothed with many setæ, which increase somewhat in length from the base outwards, and the distal ones are slightly more than half as long as the depth of the cerci. The terminal area looks outwards and somewhat upwards; it is a little shorter

than the longest lateral setæ. The apical seta is slightly longer than the distal lateral ones.

Length.—3 to 4.2 mm.

Locality.—Island Koh Chang (Gulf of Siam), under stones, January 17th, 1900 (Dr. Th. Mortensen).

Remarks.—This species is sharply separated from the following one, *S. pauperata*, by the characters pointed out in remarks on the last-named species; from the other species of the genus it is easily distinguished by the characters limiting Group III, and put forward above on pp. 25, 26.

12. *Scutigerella pauperata*, n. sp. Pl. 5, figs. 2 *a*—2 *i*.

Material.—Many specimens from a rather small island.

Head.—Seen from above it is moderately narrow in proportion to the length, with the lateral margin rather flatly arched without any angle; the longest lateral seta as long as or a little longer than the breadth of the basal antennal joints. The central rod is rather short, the anterior part with its branches being not visible, and posteriorly it is connected with the vertex of a triangle which is not very conspicuous, and limited on the sides by the oblique rods, which are feebly developed.

Antennæ.—The number of joints varies from nineteen to thirty-two. Seen from the side the basal third of the antennæ, especially the second to the sixth joint, is thickened, but in a somewhat less degree than in *Scut. crassicornis*; on the inner side of the second to the sixth or seventh joint two or three setæ on the inner side are very elongate, the longest of them two and a half to three times longer than the outer setæ, and besides nearly vertical on the longitudinal axis of the antennæ. The secondary whorl begins below on the seventh or eighth joint, but is developed only on the ventral side of all the following joints (fig. 2 *a*). The setæ in the central whorl are rather long on the upper side and considerably shorter below. Near the distal two thirds of the joints a rather robust, conical, small rod is

found on the upper side in front of the central whorl, as in *S. crassicornis*. The terminal joint (fig. 2 *b*) has the usual striped sense-organ rather small, with the stalk shorter than the striped portion, and (fig. 2 *c*) another organ besides, which is more or less thick, clavate, and somewhat curved.

Scuta.—The second scutum (fig. 2 *d*) is posteriorly produced into a pair of very small, acute processes, and the margin between these angular projections is flatly concave; the antero-lateral setæ, which are directed outwards and somewhat forwards, are very long, much longer than the breadth of the proximal antennal joint. Of the other marginal setæ very few are short, and two of the lateral pairs are even long; the longest of these pairs are nearly two thirds as long as the antero-lateral setæ, but directed much backwards. All scuta from the first to the twelfth (both included) each with a very long pair of setæ corresponding to the antero-lateral one in the second scutum, and, if not disturbed, directed essentially outwards; on the longer ones of the scuta at least one pair of long lateral setæ are also found. The penultimate scutum posteriorly emarginate, with the angular projections very small or scarcely visible, and with a postero-lateral pair of long setæ. The last scutum posteriorly with an oblong, median, deep depression.

Legs.—The last pair (fig. 2 *e*) are robust, especially in large specimens. In these the metatarsus is only one third longer than deep, and the tarsus, which widens strongly towards the base, is slightly more than two and a half times longer than deep. The metatarsus with three and the tarsus with five setæ in the anterior dorsal row; these setæ on the tarsus are rather long, and the two distal ones on the metatarsus somewhat longer, also a distal dorsal seta is inserted behind the anterior row on the metatarsus, and this seta is two thirds as long as the depth of its joint; a similar long seta is placed distally on the tibia. The anterior claw (fig. 2 *f*) is moderately developed in all respects; the posterior claw is somewhat more slender, more curved, and reaches to or a little beyond the proximal two thirds of the

other; the front seta is rather short and weak. The exopods are very short, generally nearly impossible to discover. The last pair of legs is a little more robust than the eleventh pair, which are more robust than the tenth; the ninth has the tarsus slender. In small specimens with the full number of legs the last pair of legs are less robust and the tarsus more slender, but scarcely in so high a degree as in the species described above. The first pair of legs (fig. 2 *g*) with the claws (fig. 2 *h*) somewhat more slender than those on the posterior legs, otherwise rather similar as to shape and relative length; the front seta is moderately developed.

Cerci (fig. 2 *i*).—Short and robust, about three times longer than deep, with the distal part somewhat produced (often a little more than in the specimen figured). They are set with a very moderate number of setæ, which gradually but considerably increase in length from the base outwards; the distal ones rather thin, and more than half as long as the depth of the cerci. The terminal area looks outwards, and is a little shorter than the distal setæ. The apical seta is as long as or a little longer than the longest lateral setæ, but more robust towards the base.

Length.—1·9 to 2·7 mm.

Locality.—Isl. Koh Chang (Gulf of Siam): under stones, January 7th and 12th, 1900; under plants on stones, January 6th, 1900. All collected by Dr. Th. Mortensen.

Remarks.—This species is distinguished from all other forms of the genus by the extreme shortness of the exopods. It is rather allied to *S. crassicornis*, but easily distinguished from it by the very long antero-lateral setæ on the scuta, by the long dorsal setæ on the posterior legs, by the short cerci with a very moderate number of setæ, etc.; in the elongate vertical setæ on the inner side of the proximal antennæ it agrees essentially with *S. crassicornis*, but differs from the other species of the genus.

Spurious or insufficiently described Species.

1. *Scut. gratiæ*, Ryder.—This name, without description, was given by Ryder in 'The American Naturalist,' xiv, p. 375, 1880; the next year he described and figured the species in 'Proceed. of the Acad. of Natur. Sciences of Philadelphia,' 1881, p. 375. He had captured specimens in "Fairmount Park, Philad.; Havre de Grâce, Md.; Washington, D.C.; Franklin Co., Pa." It is impossible to decide whether it is identical with the European *Scut. nivea* (Scop.) or a distinct species.

2. *Scolopendrella latipes*, Scudder ('Proceed. Boston Soc. Nat. Hist.,' vol. xxii, 1882-3, pp. 64, 65).—This species was established on one specimen, which was crushed before the examination had been finished; it had been captured near Boston. The description of the scuta makes it clear that it belonged to *Scutigera*, but the author's statement "there are no hairs upon the body" (p. 65) shows evidently that the specimen had been badly preserved, the hairs on the scuta being lost. The statement "seven abdominal joints, each with a pair of legs," seems to indicate that the specimen had possessed in all only ten pairs of legs and was immature; it measured 3 mm. in length. The description and the drawing (fig. 5) of the antennæ show clearly that they had been strongly contracted; the description and the drawings (figs. 2 and 3) of the legs can scarcely be understood without assuming that these appendages had been compressed by contraction or shrivelling. It is impossible to discover in the whole description more than one valuable character, viz. the shortness of the "parapodia;" but this is, of course, not sufficient for a recognition of the species, and I think I can pronounce with certainty that it will never be found again. It will therefore be practical to cancel it completely.

Gen. 2. *Scolopendrella*, Gervais.

The characterisation of this genus has been given above on p. 24, and some supplementary notes have been added immediately after the diagnosis.

CONSPECTUS OF THE SPECIES.

It may be practical to divide the genus into three groups, and then to produce a key of the species of each group.

A. The first pair of legs contain three free and very distinct joints (the trochanter not included); the tarsus terminates in two conspicuous claws.

a. The scuta have the hind margin between their processes provided with a transverse belt adorned with numerous longitudinal stripes. The cerci without transverse stripes on the most distal part opposite to the terminal area. The head with the central rod interrupted in front of the middle, where there is a pair of very short lateral branches (while the anterior branches are scarcely perceptible). The first pair of legs more than two thirds as long as the second pair, and of normal shape Group I.

b. The scuta have the hind margins simple, without any striped belt. The cerci with several transverse elevated lines across the distal part opposite to the terminal area. The head has the central rod without lateral branches in front of the middle. The first pair of legs at most about half as long as the second pair, considerably reduced and deviating from normal legs as to the length and shape of the joints Group II.

B. The legs of the first pair rudimentary, each leg being a wart-like protuberance without claws Group III.

Species of Group I.

Three of the characters pointed out in the key, viz. the development of the first pair of legs, the absence of trans-

verse lines on the distal part of the cerci, and the secondary lateral branches from the central rod of the head, are not met with in any other species of the genus; in the two first-named features this group agrees with the genus *Scutigere*lla. Only one species is known . . . 1. *S. notacantha*, Gerv.

Species of Group II.

a. Nearly all the setæ on the antennæ are very conspicuously pubescent, and also thick from the base to near the acuminate end . . . 2. *S. microcolpa*, Muhr.

b. All setæ on the antennæ naked, slender, and tapering from the base to the end.

a. The legs of the first pair robust, and longer than the tarsus of the last pair. The cerci considerably shorter than the last pair of legs, with rather few setæ, and the terminal area nearly as long as their depth . . . 3. *S. subnuda*, n. sp.

β. The legs of the first pair rather slender, and shorter than the tarsus of the last pair. The cerci slightly longer than the last pair of legs, with a very large number of setæ, and the terminal area nearly three times shorter than their depth. . . . 4. *S. Silvestrii*, n. sp.

Species of Group III.

A. All setæ on the antennæ naked and slender.

a. The last pair of legs with two or three long protruding dorsal setæ on the metatarsus, and at least three similar setæ in the anterior dorsal row on the tarsus. The terminal area on the cerci looks downwards.

a. The last pair of legs with three long protruding dorsal setæ on the metatarsus, and four to five in the anterior dorsal row on the tarsus. The cerci rather large and densely clothed with setæ. (The second scutum with its antero-lateral setæ considerably or very much shorter than its processes.)

§. The cerci with many of the setæ long and protruding in all directions 5. *S. Isabellæ*, Grassi.

§§. The cerci with a small number of setæ on the lower side long and protruding, while all the other are short.

6. *S. texana*, n. sp.

β. The last pair of legs with two long protruding dorsal setæ on the metatarsus, and three in the anterior dorsal row on the tarsus. The cerci of middle length or rather short, with at most a rather moderate number of setæ.

§. The second scutum with the antero-lateral setæ a little shorter to a little longer than the processes.

†. The second scutum has the distance between its processes considerably longer than their length; the distance between the processes of the third scutum twice as long as their length 7. *S. vulgaris*, n. sp.

††. The second scutum has the distance between its processes from a little to considerably shorter than their length; the processes of the third scutum at most nearly one half longer than their length.

*. The cerci with long setæ only on the lower part of the outer side. The antennæ with the secondary whorl complete on more than half of the joints. Rather larger American species 8. *S. neotropica*, n. sp.

**. The cerci with some long setæ spread on the whole outer surface. The antennæ with the secondary whorl complete only on the joints of their distal third. Small species from Further India 9. *S. simplex*, n. sp.

§§. The second scutum with the antero-lateral setæ not half as long as its processes 10. *S. pusilla*, n. sp.

b. The last pair of legs with only one long protruding dorsal seta on the metatarsus, and two similar setæ in the anterior row on the tarsus. The terminal area of the cerci looks outwards 11. *S. brevipes*, n. sp.

B. Most of the setæ on the antennæ plumose and very thick (the terminal area on the cerci looks outwards).

12. *S. antennata*, n. sp.

GROUP I.

1. *Scolopendrella notacantha*, Gervais. Pl. 5,
figs. 3 *a*—3 *k*.
1844. *Scolopendrella notacantha*, Gervais, 'Ann. d. Sci. Natur.,' ser. 3, Zool., T. ii, p. 79, pl. 5, figs. 15—18.
1847. *S. notacantha*, Gervais, 'Hist. Nat. d. Insectes Aptères,' iv, p. 301, pl. 39, figs. 7—7 *E*.
1886. *S. notacantha*, Grassi, 'Mem. d. Reale Accad. d. Sci. di Torino, ser. 2^a, t. xxxvii, p. 594.

(The animals described by Latzel, Muhr, and Berlese as *S. notacantha*, Gerv., do not belong to this species.)

Material.—Many specimens from two localities.

Head (fig. 3 *a*).—Moderately long, about one fourth longer than broad. The central rod apparently interrupted a little outside its middle, and here provided with short lateral branches; slightly in front of these branches the rod is again very plain, but more narrow, and the frontal branches are scarcely perceptible.

Antennæ.—They contain fifteen to eighteen joints. All setæ in the central whorls naked and tapering from the base to the end; on the five or six most proximal joints the setæ on the inner side are somewhat longer than on the outer side, and directed much forwards. A secondary whorl begins below a little before the middle of the antennæ, but it is not developed on the upper half of any of the distal joints (fig. 3 *b*).

Scuta.—The second scutum (fig. 3 *c*) with the hind margins between the terminal part of the processes nearly semicircular, and adorned with a transverse band with numerous sharp longitudinal stripes; the processes are a little longer than broad at the base, with one rather long seta near each margin besides the subapical one; the antero-lateral setæ are very long, rather considerably longer than the length of

the processes; all the lateral setæ are proportionately long, and the longest pair are especially elongate and only somewhat shorter than the antero-lateral pair. The third scutum with the striped band as in the preceding; the processes somewhat broader than long, each with three setæ as in the second scutum, and the basal distance between them about twice as long as their length; the antero-lateral setæ as in the second scutum, and the lateral setæ proportionately long, but none of them especially elongate. The striped transverse band is developed on the hind margin of all scuta armed with processes. All scuta, the last one excepted, with one pair of setæ as long as the antero-lateral setæ on the second scutum, and some of them—for instance, the eleventh scutum (fig. 3*d*)—besides with a pair of lateral setæ, only somewhat shorter than the antero-lateral pair.

Legs.—The last pair (fig. 3*e*) is rather short and robust; the tibia and the metatarsus each with one distal dorsal protruding seta, which is very long, nearly as long as the depth of their joints. The tarsus is scarcely four times longer than deep, with three protruding setæ in the anterior dorsal row, and these setæ are very long, the intermediate one even considerably longer than the depth of the joint. The claws (fig. 3*f*) are slender, the posterior one somewhat shorter, but only a little more curved and slender than the other; the front seta is rather short. The first pair (fig. 3*g*) are well developed, more than two thirds as long as the second pair; the femur is somewhat longer than deep; the upper margin of the tibia is considerably longer than the depth of the joint, the tarsus more than three times longer than deep; the claws are well developed (fig. 3*h*), the anterior rather long and curved, the posterior considerably shorter, besides more curved, more slender, and articulated to the prætarus in such a way that it diverges extremely from the other claw; the front seta of middle length and rather robust.

Cerci (fig. 3*i*).—Of very moderate size, slightly longer than the three distal joints of the last pair of legs, nearly conical, from three and a half times to four times longer

than deep, set with rather few setæ, of which two or three near the terminal area are rather long, the others somewhat shorter, and scarcely more than half as long as the depth of the cerci. The terminal area looks obliquely upwards and outwards; it is rather long, more than two thirds as long as the depth of the cerci, and adorned with a system of partly somewhat irregular longitudinal lines (fig. 3 *k*); the terminal surface outside this plan without transverse lines. The apical seta as long as or a little longer than the terminal plan, and robust at the base.

Length.—3 to 3·4 mm.

Locality.—Rome, fifteen specimens (Dr. F. Silvestri); Aspromonte in Calabria, in a forest about 4500 feet above the level of the sea, twelve specimens (the author).

Distribution.—Judging from the length of the first pair of legs on the fig. 16 in ‘Ann. d. Sc.’ referred to above, it must be this species which has been drawn and described by Gervais; it can be added that he writes that the antennæ of his animals could contain more than fourteen joints, “vingt même dans l’état complet;” and this last statement strengthens the opinion that it is our *S. notacantha*, and not the species established later on by Muhr as *S. microcolpa*, which he has examined. He had collected his specimens mentioned in a garden in Paris, and in the environment of the same town. Grassi states (p. 596) that he has captured the species at Rovellasca (in the province of Como), near Lecco; at Sparanisi, near Capua; and at Catania. On p. 594 he mentions the setæ which I have named the antero-lateral pair, and this statement proves that at least the animals especially examined by him have belonged to *S. notacantha*, and not to *S. microcolpa*. All other localities out of Italy mentioned in the literature are uncertain or incorrect, and in the present state of knowledge it is impossible to say more on the distribution of this species.

Remarks.—This very interesting species is easily distinguished from all other forms hitherto known by the characters set forth in the analytical key for the groups.

The length of the antero-lateral setæ separates it also from all other European species of this genus.

GROUP II.

2. *Scolopendrella microcolpa*, Muhr. Pl. 5,
figs. 4 *a*—4 *h*; Pl. 6, figs. 1 *a*, 1 *b*.

1881. *Scolopendrella microcolpa*, Muhr, 'Zoolog. Anzeiger,' No. 75, p. 59, figs. 1, 2, and 4.

Material.—Six specimens from one locality, all with the full number of legs.

Head (fig. 4 *a*).—Moderately long, about one fourth longer than broad. The central rod with a sharp transverse suture at the middle, without vestige of lateral branches, but the frontal branches are strongly developed.

Antennæ.—They were complete in two specimens, and contained respectively twenty-three to twenty-five, and twenty-six to twenty-seven joints. The setæ in the central whorls (fig. 4 *b*) are thick and subcylindrical nearly to the acuminate and somewhat produced end, besides they are very conspicuously pubescent; on the inner side of the eight or ten proximal joints two or three naked and slender setæ are inserted in each central whorl instead of the thick setæ. The thick setæ on the proximal joints twice as long as those on the most distal joints (fig. 4 *c*). The joints in the distal half of the antennæ with one seta to three setæ on the lower side as a rudiment of a secondary whorl; these setæ are similar in shape, but not half as long as those in the central whorl; the terminal joint has its distal half set with a number of pubescent and thick setæ.

Scuta.—The second scutum (fig. 1 *a*) with the hind margin nearly straight between the inner base of its processes, and without any striped band; the processes scarcely as long as broad, with three to four moderately short setæ along each margin, and the distal seta inserted a little from

the apex; the distance between the processes as long as their length. The antero-lateral setæ are rather short, not half as long as the processes; one of the lateral setæ a little shorter than the antero-lateral pair. The third scutum (fig. 1 *a*) with the hind margin as in the second; the processes one half broader than their length, with the same number of setæ at the margins; the antero-lateral setæ subsimilar to those on the preceding scutum; the distance between the processes is a little shorter than their breadth. The other scuta present nothing of special interest.

Legs.—The last pair (fig. 4 *d*) present characteristic features. The tibia with two, the metatarsus with three protruding dorsal setæ, which at most are a little more than half as long as the depth of their joints; the tarsus is elongate, unusually slender, nearly six times longer than deep, with five protruding setæ in the anterior dorsal row, and most of them about as long as the depth of the joint. The anterior claw (fig. 4 *e*) moderately slender and rather curved, the posterior slightly more slender, and only a little shorter than the other; the front seta rather short and thin. The first pair (fig. 4 *f*) scarcely one third as long as the second pair, and considerably shorter than the tarsus of the last pair; femur and tibia each a little deeper than long; the tarsus nearly twice as long as deep, terminating in two claws (fig. 4 *g*), the anterior of which is a little longer than the other, and both are rather curved and distally slender; the front seta rather short and thin.

Cerci (fig. 1 *b*).—Rather long, only a little shorter than the last pair of legs, somewhat more than four times longer than deep, clothed with a large number of setæ differing considerably in length; the long setæ are rather numerous, and spread on the outer surface both above and below; they are protruding, and not quite half as long as the depth of the cerci, while the other setæ are rather depressed and considerably shorter. The terminal area is short, half as long as the depth of the cerci, and looks outwards (and slightly downwards); on the opposite side the surface has seven to

ten fine thickened transverse lines. The apical seta is short, scarcely as long as the terminal area.

Length.—The largest one of my few specimens is considerably extended, and measures 3.2 mm. in length; the shortest specimen, which has all pairs of legs well developed, is rather contracted, and measures 1.7 mm.

Locality.—Palmi in Calabria, where the specimens have been captured in May, 1893, by the author, in a wood of olive trees.

Distribution.—The only locality previously known is Prague in Bohemia, where Muhr collected the animals on which he established the species. His description and figures are far from good, but he says on the joints of the antennæ that they are “mit einigen kreisförmig angeordneten, kurzen, steifen Borsten besetzt, die selbst wieder ihrer ganzen Länge nach mit Spitzen versehen sind;” and this last feature is not met with in any other European species known to me; besides, he mentions the first pair of legs in a way which agrees well with my specimens. According to Latzel (op. cit.), Muhr withdrew his new species (in a paper unknown to me) as synonymous with *S. notacantha*, Gerv., one year after he had established it, but it was necessary to re-establish it.

Remarks.—By the setæ of the antennæ this species is easily separated from all other European forms. The shape of the second and third scuta and their setæ, the tarsus of the last pair of legs, the first pair of legs, and the cerci present other excellent characters.

3. *Scolopendrella subnuda*, n.sp. Pl. 6, figs. 2 *a*—2 *g*.

Material.—Six adult specimens from two countries.

Head.—A little more narrow in proportion to its length than in *S. microcolpa*; the central rod as in that species, but the frontal branches are scarcely visible.

Antennæ.—They contain from fifteen to twenty joints. The setæ in the central whorls are all slender and tapering

from the base, rather short on the proximal and very short on the most distal joints; in the distal half of the antennæ two or three minute setæ (fig. 2 *a*) are found on the lower side behind each central whorl, and only on the subapical joint a single seta of this rudimentary secondary whorl has been developed on the upper side.

Scuta.—The second scutum (fig. 2 *b*) with the posterior margin between the processes feebly curved and without any striped band; the processes are narrow and distally produced, considerably longer than broad; a single short seta is found on each side slightly in front of each process which has no setæ along the lateral margins, while the subapical seta is inserted rather near the end. The distance between the processes is one half longer than their length. Each lateral margin of the scutum with four setæ in all, of which the antero-lateral one is about half as long as the processes and the other short. The third scutum (fig. 2 *b*) rather similar to the second: the processes are somewhat longer than broad, the three setæ in front of their base and near the end as in the preceding scutum, the basal distance between the processes twice as long as their length; each lateral margin with two setæ in all, one of which is near the process, and the other, the antero-lateral one, is a little shorter than that on the second scutum.

Legs.—The last pair (fig. 2 *c*) is rather robust. Tibia and metatarsus each with a distal dorsal protruding seta, which is somewhat shorter than the depth of the last-named joint. The tarsus is a little more than three times longer than deep, with a dorsal protruding seta, a little longer than the depth of the joint, inserted at the middle, and with this in the anterior row only a single subapical seta which is somewhat shorter than the other. The claws (fig. 2 *d*) are rather slender, the posterior one nearly as long as the other; the front seta is short. The first pair (fig. 2 *e*) about half as long as the second and somewhat longer than the tarsus of the last pair. The femur is about as long as deep, the tibia a little longer than deep and as long as the tarsus, which is nearly twice as

long as deep; the anterior claw is rather robust and much curved (fig. 2 *f*), considerably longer than or nearly twice as long as the other.

Cerci (fig. 2 *g*).—Rather short, somewhat shorter than the last pair of legs, from a little more than three times to four times longer than deep, and decreasing slightly in depth from the base to near the terminal area; they are set with rather few setæ, somewhat unequal in length, and the longest distal ones somewhat shorter than the depth of the cerci. The terminal area is long, only a little shorter than the depth of the cerci, and looks downwards; the surface above the area with about seven coarse transverse lines (consisting as usual of minute spines). The apical seta is as long as or somewhat longer than the depth of the cerci.

Length.—The largest specimen is extended, and measures 1.75 mm., a small but adult specimen 1.2 mm.

Locality.—Palmi, Calabria, four specimens captured (by the author) together with *S. microcolpa*, and a fifth specimen was taken (by Mr. C. Börner) at Catania or at Palmi, besides one specimen from Marburg, Germany (Mr. C. Börner).

Remarks.—This small species is easily separated from the other species of the group by the very few setæ at the margins of the scuta, by the shape of the cerci and their few setæ, finally by the legs.

4. *Scolopendrella Silvestrii*, n. sp. Pl. 6, figs. 3 *a*—3 *g*.

Material.—Three adult specimens, and one specimen with eleven pairs of legs.

Head.—Elongate, nearly one half longer than broad. The central rod interrupted at the middle, its most anterior part and the anterior branches evanished.

Antennæ.—The number of joints in four complete antennæ varies from seventeen to twenty-two. The setæ in the central whorls (fig. 3 *a*) are all slender, tapering from the base and naked, moderately short on the proximal and short

on the distal joints. A second whorl begins below about at the middle of the antennæ, and nearly on the distal third of the appendages a seta is found near the upper margin, but the whorl is not complete on the outer side of any of the joints.

Scuta.—The second scutum (fig. 3 *b*) with the hind margin between the processes nearly straight and without any striped band; the processes are narrow and distally exceedingly produced, nearly one half longer than broad, with two setæ at the basal part of the outer margin, one subbasal seta at the inner margin, and the usual distal seta inserted very far from the end. The distance between the processes slightly shorter than their length. Each lateral margin of the scutum with about seven setæ in all; the antero-lateral one is several times shorter than the processes, and the other setæ are short. The third scutum with the processes somewhat shorter, a little longer than broad, the distance between them somewhat longer than their length, six setæ in all (the distal one as usual not included) along each lateral margin, otherwise essentially as the second scutum.

Legs.—The last pair, which is similar to the penultimate pair (fig. 3 *c*), is moderately robust. The tibia with a distal dorsal seta about half as long as the depth of the joint; metatarsus with two similar setæ in the anterior dorsal row. The tarsus a little more than three times longer than thick; in the anterior row three protruding setæ as long as or slightly longer than the depth of the joint. The anterior claw (fig. 3 *d*) moderately short and robust, a little longer than the other; the front seta is short. The first pair (fig. 3 *e*) not one third as long as the second, and somewhat shorter than the tarsus of the last pair of legs; femur and tibia shorter than deep, the tarsus somewhat longer than thick (fig. 3 *f*); the claws are well developed, much curved, and subequal in length.

Cerci (fig. 3 *g*).—They are even longer than the last pair of legs, very robust, and nearly four times longer than deep, decreasing much in depth in the distal third. They are

rather densely clothed with setæ, the major part of which are rather short and depressed, while many are strongly protruding in all directions, considerably longer than the others and in some cases half as long as the depth of the cerci. The terminal area is very small, nearly three times shorter than the depth of the cerci, and looks outwards and a little downwards; the surface on the opposite side with some few transverse lines. The apical seta is exceedingly short, even much shorter than the terminal plan.

Length.—An extended specimen measured 1·8 mm.; the two other adult specimens are nearly of the same length.

Locality.—S. Ana, Misiones, Argentina, July 27th, 1900, three specimens (F. Silvestri); Tacurù Pucù (Alto Paraná), Paraguay, July 6th, 1900, one immature specimen (F. Silvestri).

Remarks.—This species is sharply separated from the other forms by the shape of the second scutum, shape and clothing of the cerci, and the first pair of legs. The name has been chosen in honour of Dr. F. Silvestri, who has collected not only this and some others of the species described in this paper, but, besides, several interesting small forms of Palpigradi and Pauropoda, thereby lending a valuable assistance to me.

GROUP III.

5. *Scolopendrella Isabellæ*, Grassi. Pl. 6, figs. 4 *a*—4 *h*.

1886. *Scolopendrella Isabellæ*, Grassi, 'Mem. d. Reale Accad. d. Sci. di Torino,' ser. 2^a, t. xxxvii, pp. 594–5.

Material.—Many specimens, adults and young ones, from three localities in Southern Italy.

Head.—Rather elongate, not quite one third longer than broad. The central rod is interrupted in the middle, without lateral branches; its anterior part and the frontal branches are strongly developed.

Antennæ.—They contain from seventeen to twenty-one

joints. The setæ in the central whorl are all naked, slender and tapering from the base, moderately long on the proximal joints, but not half as long on the most distal joints. About at the end of the basal third of the antennæ the secondary whorl begins below (fig. 4 *a*) ; on the distal half of the antennæ it is also developed on the upper side, and at least on the most distal joints a seta of a third whorl protrudes from the lower margin. All the joints, with exception of a few proximal ones, with a number of clear, circular small spots on the outer side (fig. 4 *a*) ; in these spots a minute seta seems always to be inserted, but it is often so short that it is exceedingly difficult to discover.

Scuta.—The second scutum (fig. 4 *b*) with the hind margin between the processes nearly straight, and without striped band. The processes are rather large, nearly regularly triangular, scarcely broader than long, with about four setæ along each margin and the usual distal seta near the end. The distance between the processes is much shorter than their length. The antero-lateral setæ are about of middle length, at least somewhat shorter than processes ; among the other moderately numerous lateral setæ two pairs are of moderate length. The third scutum (fig. 4 *b*) has the processes somewhat shorter than broad, but they are only half as long as the distance between them, with about three setæ along each margin ; the antero-lateral setæ as those on the second scutum.

Legs.—The last pair (fig. 4 *c*) are proportionately rather long. The tibia with two dorsal protruding setæ slightly more than half as long as the depth of the joint ; the metatarsus with three rather similar setæ in the anterior dorsal row, all somewhat or considerably shorter than the depth of the joint. The tarsus rather long, four and a half times longer than deep, generally with five, and at least with four protruding setæ in the anterior dorsal row, and the setæ at most a little longer than the depth of the joint. The anterior claw (fig. 4 *d*) is rather long, moderately robust and curved, somewhat longer and thicker than the other ; the front seta of

middle length. The first pair (fig. 4e) are oblong, irregularly shaped knobs, with hairs and very few long setæ.

Cerci (fig. 4f).—They are rather long, slightly shorter than the last pair of legs, about four and a half times longer than deep, densely clothed with setæ, many of which are protruding in all directions and almost half as long as the depth of the cerci, while the others are considerably shorter and depressed. The terminal area is a little more than half as long as the depth of the cerci, and looks downwards, the surface above it (fig. 4g) with about ten sharply prominent lines. The apical seta as long as or a little longer than the area.

Length.—2·3 to 3·5 mm.

Locality.—Calabria: Scilla, four specimens taken (by the author) in June, 1893, in a copse about 1000 feet above the level of the sea; Aspromonte, in a forest about 4500 feet above the level of the sea (the author). Furthermore, a good number of specimens have been secured (by Mr. C. Börner) either at Palmi in Calabria or, more probably, Catania in Sicily.

Remarks.—This species is rather allied to *S. vulgaris*, n. sp., with which it certainly has been confounded by Prof. Grassi. The differences between these two species will be pointed out in the remarks to the last-named form.

From all species with the first pair of legs rudimentary it is separated by the clothing and shape of the cerci, and, *S. exana* excepted, besides by the number of dorsal setæ on the two distal joints of the posterior legs.

It may be possible that some of the specimens collected by Latzel, v. Attems, etc., and referred by them to *S. notacantha*, in reality belonged to this species, and not to *S. vulgaris*, n. sp. (see below), but on this topic nothing can be said with the slightest degree of certainty. Furthermore, it is impossible to state with absolute certainty if the animals upon which Grassi established his *S. Isabelle* in reality belonged to our species with this name or to *S. vulgaris* or to both combined, but the last-named circum-

stance is the most probable. When Grassi (p. 596) states that he has captured *S. Isabellæ* at Rovellasca (near Como), near Lecco, near Capua, and at Catania, it can be taken as certain that he has had specimens of both species. I have referred the name *S. Isabellæ* to the species described above, as it seems to be common at Catania. Mr. Börner, who has captured many specimens of this species, but very few of *S. vulgaris*, has labelled his animals "Catania, Palmi," but I have not found it at Palmi, and suppose, therefore, that Mr. Börner has captured his specimens of *S. Isabellæ* near Catania.

6. *Scolopendrella texana*, n. sp. Pl. 6, figs. 5 *a*—5 *e*.

Material.—Two adult specimens.

Head.—Rather elongate, not quite one third longer than broad. The central rod as in *S. Isabellæ*, interrupted at the middle, and having the anterior part and the frontal branches strongly developed.

Antennæ.—They contain nineteen to twenty-two joints. The central whorl nearly as in *S. Isabellæ*; a second whorl begins below on the fifth or sixth joint, and a little before the middle of the antennæ it is complete on the outer surface and above; the joints in nearly the distal half of the antennæ (fig. 5 *a*) possess besides some setæ of one or two other whorls on the lower outer part between the two complete whorls, so that the lower half of the outer side has a rather considerable number of short setæ, and the distance between the central and the secondary whorl is unusually long.

Scuta.—The second scutum (fig. 5 *b*) with the hind margin between the processes straight, and without striped band; the processes are large, slightly longer than broad, with about four setæ along each margin, and the usual distal seta near the end. The distance between the processes is considerably shorter than their length. The antero-lateral setæ are rather short, not half as long as the processes, the lateral setæ from the antero-lateral pair to the end of the processes

rather numerous and short. The third scutum with the processes considerably broader than long, the distance between them about equal to their length, and the setæ nearly as on the preceding scutum.

Legs.—The last pair (fig. 5 *c*) are proportionately rather long. The tibia with two, the metatarsus with three protruding setæ in the anterior dorsal row, none of them quite as long as the depth of the tarsus. The tarsus is rather long, about five times longer than deep, with four protruding dorsal setæ in the anterior row, and the longest seta about as long as the depth of the joint. The anterior claw (fig. 5 *d*) is elongate, moderately robust and rather curved; the posterior claw is considerably more slender, more curved, and nearly one third shorter than the other; the front seta long and rather thick. The first pair are exceedingly small rounded knobs with some short setæ.

Cerci (fig. 5 *e*).—Robust and rather long, somewhat longer than the last pair of legs, slightly more than four times longer than deep, and about as broad as deep. They are set with many setæ, of which about seven on the lower side are strongly protruding, moderately long, yet nearly two and a half times shorter than the depth of the cerci; all other setæ are considerably shorter and depressed. The terminal area is scarcely half as long as the depth of the cerci, and looks downwards; the striped surface above it is very short, with six or seven thickened lines. (The apical setæ are wanting in my specimens.)

Length.—2.8 mm.

Locality.—Austin, in Texas (collected by Prof. W. M. Wheeler).

Remarks.—The species is allied to *S. Isabellæ*, Grassi, but easily separated by the cerci, especially by the complete want of longer and protruding setæ on the upper two thirds of their outer surface.

7. *Scolopendrella vulgaris*, n. sp. Pl. 6, figs. 6 *a*—6 *d*;
Pl. 7, fig. 1 *a*.

1884. *Scolopendrella notacantha*, Latzel, 'Die Myriop.
d. österr.-ungar. Monarchie,' ii, p. 11 (at least
partly).

Material.—Many specimens from various countries.

Head.—In all respects as that of *S. Isabellæ*.

Antennæ.—They contain fifteen to twenty-one joints. As to the central whorls, they differ scarcely from those of *S. Isabellæ*, but the secondary whorl begins at the middle of the antennæ, and only on a few distal joints is it developed on the upper side; on these distal joints three setæ can be seen on the lower margin. The joints present very few clear circular spots on the outer side.

Scuta.—The second scutum (fig. 1 *a*) with the hind margin between the processes straight and without transverse band; the processes are of moderate size, a little longer than broad, along the inner margin with two setæ, one of which is inserted even just in front of the base, and three setæ at the outer margin, while the distal seta is seen near the end. The distance between the processes is somewhat longer than their length. The antero-lateral setæ nearly as long as or a little longer than the processes; from the antero-lateral seta to the apical one there are six or seven moderately or rather long setæ. The third scutum (fig. 1 *a*) has the processes a little shorter than broad, with two or three setæ along each margin, the distance between the processes at least twice as long as their length; the antero-lateral setæ as on the second scutum.

Legs.—The last pair (fig. 6 *a*) a little shorter than in *S. Isabellæ*. The tibia and metatarsus each with two protruding dorsal setæ, and the longest seta at most nearly as long as the depth of the metatarsus. The tarsus not quite four times longer than deep, with three protruding setæ in the anterior dorsal row, and these setæ are about as long as

those on the preceding joint. The claws do not present any character distinguishing them from those in *S. Isabellæ*; sometimes they are shaped as in that species, and sometimes they are shorter and less acuminate (fig. 6 *b*). The first pair (fig. 6 *c*) are minute knobs with at least one long seta and some shorter setæ or hairs.

Cerci (fig. 6 *d*).—They are of middle size, rather considerably shorter than the last pair of legs, slightly more than four times longer than deep. They are set with a moderate number of setæ, of which three or four at the lower margin are strongly protruding and only a little shorter than the depth of the cerci, while the others are considerably shorter, slightly or not more than half as long as the depth of the cerci, oblique, or rather depressed. The terminal area about two thirds the depth of the cerci, looking downwards; the surface above it of medium length, with seven or eight very pronounced lines. The apical seta about as long as the ventral protruding setæ.

Length.—One of the largest specimens (from Calabria) measures 3.3 mm. in length, but most adult specimens are between 2.5 and 3 mm.

Locality.—Italy: Scilla, about 1000 feet above the level of the sea, in a copse, June 24th, 1893, six specimens (the author); Aspromonte, in a forest, about 4500 feet above the level of the sea, June 25th, 1893, ten specimens (the author); Palmi or Catania, four specimens (Mr. C. Börner). Helvetia: Luzern, in a wood, July 12th, 1893 (the author). Germany: Tübingen, one specimen (Dr. F. Meinert); Marburg, two immature specimens (C. Börner). Denmark: Copenhagen, in the Royal Garden, "Rosenborg Have," under large flower-pots which had been buried in the earth to the upper margin, July 16th, 1901, several specimens (the author).

Remarks.—This species is allied to *S. Isabellæ*, but is sharply distinguished by three characters: the last pair of legs have two protruding dorsal setæ on the metatarsus and three in the anterior row on the tarsus, while the correspond-

ing joints in *S. Isabellæ* have respectively three and four or five setæ; the cerci have only half as many setæ as in *S. Isabellæ*, and only a few of them at the lower margin are long and protruding, while in *S. Isabellæ* a good number of rather long setæ protrude in all directions; the distance between the processes of the second scutum is somewhat longer than the processes, while it is much shorter than these in *S. Isabellæ*; some minor differences can be derived from the descriptions. Of both species I have examined specimens which had not acquired the full number of legs, and it was not difficult to separate them with absolute certainty. Most European specimens mentioned in the literature as *S. notacantha*, Gerv., and some of the specimens considered by Grassi as *S. Isabellæ* (see above), certainly belonged to this species, which seems to be so common and so widely distributed in Europe that the name *S. vulgaris* will probably be deemed appropriate.

8. *Scolopendrella neotropica*, n. sp. Pl. 7, figs.

2 *a*—2 *g*.

Material.—Two adult specimens, and a third one in which the last pair of legs have not been developed.

Head.—Only a little or very little longer than broad. The central rod is interrupted at the middle; its anterior part is conspicuous but narrow; the frontal branches are thin.

Antennæ.—In the two adult specimens they contain eighteen and twenty-one joints. The setæ in the central whorls are naked, slender, and tapering from the base, rather long on the proximal joints (fig. 2 *a*), and scarcely half as long on the most distal joints; the setæ on the inner side of the second, third, and fourth joints are about twice as long as those on the outer side. The secondary whorl begins on the lower half of the outer side on the fifth or sixth joint; on the eighth or ninth joint it is completely developed on the upper half (fig. 2 *a*, representing the seventh joint, shows

a transition stage), and on the distal half of the antennæ the setæ in the second whorl are slightly shorter than those in the central one. Setæ belonging to a third whorl have not been observed with certainty on the most distal joints.

Scuta.—The second scutum (fig. 2 *b*) with the hind margin between the processes straight, without striped band; the processes are large, a little broader than long, with three or four rather long setæ along each margin and the distal seta near the apex. The distance between the processes is much shorter than their length. The antero-lateral setæ are long, as long as or a little longer than the processes; between the antero-lateral and the apical setæ seven or eight setæ are inserted, of which two pairs are long and one of them even only slightly shorter than the antero-lateral pair, while all the other marginal setæ are rather long, longer than in any other species described here. The third scutum (fig. 2 *b*) with the processes large and much broader than long, the distance between their base subequal to their length; the setæ nearly as on the second scutum.

Legs.—The last pair (fig. 2 *c*) about as long and thick as in *S. vulgaris*. The tibia with two dorsal protruding setæ, the proximal one about half as long as the other, which is nearly as long as the depth of the joint; the metatarsus with two very protruding setæ in the anterior dorsal row, and both almost as long as or a little longer than the depth of the joint. The tarsus scarcely four times longer than deep, with three protruding setæ in the anterior dorsal row; the distal seta somewhat shorter than the two others, which are a little or rather considerably longer than the depth of the joint. The anterior claw (fig. 2 *d*) is rather long and robust, the posterior moderately slender, and nearly one third shorter than the other; the front seta of middle length. The first pair (fig. 2 *f*) are small knobs, a little longer than thick, with some hairs and two long setæ.

Cerci (fig. 2 *g*).—Rather small, about as long as the sum of the three distal joints of the last pair of legs, at most four times longer than deep, and about as broad as deep. They

are clothed with a moderate number of setæ, of which six or seven on the lower half of the outer surface, and especially at the lower margin, are strongly protruding, and about two thirds as long as the depth of the cerci, while all the others are rather depressed and considerably or much shorter. The terminal area about two thirds as long as the depth of the cerci and looking downwards; the surface above it of medium length, with seven or eight very pronounced lines. The apical seta is a little shorter than the area.

Length.—The largest of the specimens measures 3 mm.

Locality.—Rio Catouche, near Carácas (Venezuela), July 9th or 10th, 1892 (Dr. F. Meinert).

Remarks.—This species is rather closely allied to the European *S. vulgaris*, but is easily distinguished by the second scutum, the processes of which are considerably larger and much closer to each other than in *S. vulgaris*; besides, its setæ are conspicuously longer. The third scutum presents also good differences, and the antennæ, legs, and cerci present additional characters of less importance.

9. *Scolopendrella simplex*, n. sp. Pl. 7, figs. 3 *a*—3 *e*.

Material.—Nine specimens, most of them with the full number of legs, and all from one locality.

Head.—Moderately long, scarcely one fourth longer than broad. The central rod is interrupted at the middle, without lateral branches, the anterior part is moderately narrow, and the frontal branches very thin.

Antennæ.—They contain from eighteen to twenty-two joints. The setæ in the central whorls are naked, slender and tapering from the base, moderately or rather long on the proximal joints, and somewhat shorter on the distal ones. The setæ on the inner side of the joints in the proximal half of the antennæ are longer than those on the outer side, in large specimens more or less vertical to the longitudinal axis, and especially on the third to the fifth or sixth joint they are elongate, nearly twice as long as on the outer side. A little

before the middle begins the secondary whorl on the lower margin, and on the distal third of the antenna it is developed on the upper margin; the setæ of this whorl are only a little shorter than those in the central one.

Scuta.—They differ only in some rather small particulars from those of *S. neotropica*. The second scutum (fig. 3 *a*) with the processes rather large, as broad as or a little broader than long, in large specimens with three, in small specimens with two setæ along each margin, and the distal seta near the apex. The distance between the processes a little or rather considerably shorter than their length. The antero-lateral setæ as long as or a little shorter than the processes; the lateral setæ somewhat shorter than in *S. neotropica*, but yet some of them of considerable length. The third scutum (fig. 3 *a*) with the processes rather large and somewhat broader than long; the distance between them somewhat or considerably longer than their length; the setæ nearly as in the second scutum.

Legs.—The last pair (fig. 3 *b*) agree as to the number and length of the dorsal protruding setæ on the three distal joints and as to the depth of the tarsus so much with those in *S. neotropica*, that a reference to the figure and to the description of the species named is sufficient; only the claws (fig. 3 *c*) differ rather considerably: they are proportionately slender, the posterior strongly curved and slightly shorter than the other, and the front seta is rather short. The first pair (fig. 3 *d*) are small oblong knobs, with some hairs and two setæ, one of which is long.

Cerci (fig. 3 *e*).—They are somewhat shorter than the last pair of legs, slightly more than four times longer than deep, and scarcely broader than deep. They are set with a moderate number of setæ, of which eight to ten on the whole outer surface are longish or long, one on the upper side nearly as long even as the depth of the cercus, and strongly protruding downwards, outwards, or upwards; the other setæ are moderately short and depressed. The terminal area at least two thirds as long as the depth of the cerci; the surface

above it moderately long, with about eight fine lines; the apical seta is a little shorter than the area.

Length.—From 1.75 to 2.5 mm.

Locality.—Island Koh Chang, Gulf of Siam, under stones, January 12th, 1900 (Dr. Th. Mortensen).

Remarks.—The species is closely allied to *S. neotropica*, from Venezeula, but is distinguished by a number of rather small characters. The cerci have protruding setæ near the upper margin, the claws are more slender and nearly equal in length, the second scutum with the setæ a little shorter, the secondary whorl complete only on the distal third of the antennæ, etc.

10. *Scolopendrella pusilla*, n. sp. Pl. 7, figs. 4 *a*—4 *c*.

Material.—One specimen with the full number of legs.

Head.—Moderately long, scarcely one fourth longer than broad. The central rod interrupted at the middle, without lateral branches, its anterior part and the frontal branches well developed.

Antennæ.—One antenna is complete, and contains twenty-seven joints. The setæ in the central whorls are naked, slender, and tapering from the base, rather short on the proximal and short on the distal joints. The secondary whorl begins below on the fourteenth joint, but it has scarcely been developed on the upper side even on the most distal joints.

Scuta.—The second scutum (fig. 4 *a*) has the hind margin between the processes straight, without striped band; the processes are of moderate size, distally conspicuously produced, rather considerably longer than broad, with two setæ at the outer margin, one seta rather near the base of the inner margin, and the distal seta somewhat removed from the end. The antero-lateral setæ are not half as long as the processes; between these and the distal setæ five or six short setæ are inserted at the lateral margin. The third scutum

(fig. 4 *a*) with the processes slightly broader than long, less produced than those of the second scutum, but with the same number of setæ; the distance between the processes almost twice as long as their length; the antero-lateral setæ as on the preceding scutum, and only four setæ between the antero-lateral and the distal ones.

Legs.—The last pair (fig. 4 *b*) nearly as in *S. vulgaris* in several respects. The tibia with two moderately short, dorsal protruding setæ; the metatarsus with two dorsal protruding setæ in the anterior row, the distal one much longer than the other, but yet considerably shorter than the depth of the joint. The tarsus three times longer than deep, with three protruding setæ in the anterior dorsal row, all somewhat shorter than the depth of the joint. The claws moderately long, subequal in length, the anterior somewhat deeper than the slender posterior claw. (The first pair of legs, which in this group generally are difficult to observe, have not been searched for.)

Cerci (fig. 4 *c*).—A little shorter than the last pair of legs, not fully four times longer than deep. They are set with a moderate number of setæ, which differ somewhat in length from each other, but none of them are more than half as long as the depth of the cerci; some of the setæ are protruding, and the others depressed. The terminal area more than two thirds as long as the depth of the cerci and looks essentially downwards; the surface above it is rather long, with about eight conspicuous transverse lines; the apical seta nearly as long as the area.

Length.—The specimen, which is rather extended, measures 1.7 mm. in length.

Locality.—Austin, Texas (Prof. W. M. Wheeler).

Remarks.—This species is more closely allied to the European *S. vulgaris* than to any other form, but it is easily distinguished by the second scutum, the processes of which are larger and more produced, its setæ, the antero-lateral pair included, being much longer. The number of antennal joints is unusually high, considerably higher than

observed in any other species of this group, with exception of *S. antennata* (see below).

11. *Scolopendrella brevipes*, n. sp. Pl. 7, figs. 5 *a*—5 *e*.

Material.—One specimen with the full number of legs, and another with ten pairs.

Head.—Rather elongate, about one third longer than broad. The central rod interrupted at the middle and without lateral branches, its anterior part slender, and the frontal branches thin.

Antennæ.—They contain in both specimens fourteen joints, but it must be supposed that a higher number will be found in other adult specimens. The setæ in the central whorls are naked, slender, and tapering from the base, moderately long on the proximal, and considerably shorter on the distal joints. The secondary whorl begins below outside the middle of the antennæ, but is not developed above even on the most distal joints; its setæ are considerably shorter than those in the central whorls, but comparatively thick at the base.

Scuta.—The second scutum (fig. 5 *a*) with the hind margin between the processes straight, without striped band; the processes are large, considerably longer than broad, distally much produced with the terminal part very narrow; they have one seta at the outer margin, two on the basal part of the inner margin, and the distal seta rather far from the apex. The distance between the processes one half shorter than their length. The antero-lateral setæ are between half as long and one third as long as the processes; between the antero-lateral and the distal setæ four rather short setæ are inserted along the lateral margin. The third scutum (fig. 5 *a*) with the processes considerably smaller than those on the second, about as long as broad, distally somewhat produced; the distance between the processes not fully twice as long as their length; the setæ nearly as on the second scutum.

Legs.—The last pair (fig. 5 *b*) are short and slender. The tibia and metatarsus each with one protruding seta, which is nearly longer than the depth of its joint. The tarsus scarcely three and a half times longer than deep, with only two protruding setæ in the anterior dorsal row, and these setæ are considerably longer than the depth of the joint. The anterior claw is moderately robust and considerably longer than the other, which is slender and strongly curved. The first pair are small knobs, scarcely longer than thick, with two moderately long setæ (fig. 5 *c*).

Cerci (figs. 5 *d* and 5 *e*).—They are conspicuously longer than the last pair of legs, moderately large, scarcely four times longer than deep, and somewhat broader than deep. They are set with a considerable number of setæ, of which about one third are rather long, often two thirds as long as the depth of the cerci, and protruding in all directions, while the others are much shorter and depressed. The terminal area looks outwards and is exceedingly oblique, so that it is apparently one half shorter when seen from the outer side (fig. 5 *d*) than its real length, which is seen from above (fig. 5 *e*); seen from the outer side it seems to be considerably shorter than half of the depth of the cerci. The surface opposite the area is rather short, and has six or seven lines with conspicuous spines; the apical seta is nearly as long as the area.

Length.—The adult specimen measures 1.6 mm.

Locality.—Island Koh Chang, Gulf of Siam, together with *S. simplex* (Dr. Th. Mortensen).

Remarks.—This species is distinguished by some excellent characters, the second scutum having the setæ short and the processes large and strongly produced, the last pair of legs having very few protruding long dorsal setæ, and the cerci different from those of almost all other species.

12. *Scolopendrella antennata*, n. sp. Pl. 7, figs.6 *a*—6 *i*.

Material.—Eleven specimens from five localities, and several of them with the full number of legs.

Head.—Very moderately elongate, only rather little longer than broad. The central rod is not interrupted; its most anterior part and the frontal branches are thin; a strong median rod exists apparently between the posterior branches.

Antennæ.—In the adult specimens the number of joints varies from twenty-three to twenty-nine. The setæ in the central whorls, with exception of those on the inner side of the proximal joints, are very thick at the base, nearly obliquely conical, moderately short on the proximal and short on the distal joints, and all set with a number of fine hairs (fig. 6 *a*). On the inner side from the base to the fourth or to the eighth proximal joint the setæ of the central whorl are naked, very thin (fig. 6 *b*), and much longer than the thick pubescent setæ; on the following joints these thin and naked setæ become gradually much shorter and situated behind the central whorl (fig. 6 *c*), which on all sides contains only thick and pubescent setæ. The secondary whorl begins below about on the eighth joint with one short, thick, and pubescent seta; on the distal joints two or three such setæ are present below, but on the upper part of the joints the whorl is completely absent on all joints. The terminal joint with a number of very short, thick, and pubescent setæ.

Scuta.—The second scutum (fig. 6 *d*) without striped band on the hind margin. The processes are large, a little broader than long, distally somewhat produced, with the apex narrow; they have two setæ at each margin, and the distal seta is somewhat removed from the end. The distance between the processes about as long as their length. The antero-lateral setæ are slightly longer than the processes; two pairs of the lateral setæ are rather long, and the other marginal setæ of middle length. The third scutum (fig. 6 *d*)

with the processes considerably smaller than those on the second scutum, much broader than long, distally a little produced, and the distance between them nearly twice as long as their length; the setæ less numerous, otherwise nearly as on the second scutum.

Legs.—The last pair are rather short (fig. 6 *e*). The tibia with one dorsal seta, which is a little shorter than the diameter of the joint; the metatarsus with two dorsal protruding setæ in the anterior row about as long as the depth of the joint. The tarsus is not quite four times longer than deep, with three protruding setæ in the anterior dorsal row, and the two distal ones of these are somewhat longer than the depth of the joint. The claws (fig. 6 *f*) are moderately short, the anterior one rather robust, a little longer and somewhat thicker than the other; the front seta is moderately short. The first pair (fig. 6 *g*) a little longer than thick, with a small terminal acute process and about three setæ, one of which is long.

Cerci (figs. 6 *h* and 6 *i*).—Rather large, almost as long as the last pair of legs, four to four and a half times longer than deep, and especially in its proximal half considerably broader than deep. They are very densely clothed with setæ, many of which protrude in all directions, and some of them about half as long as the depth of the cerci, while the others are much shorter and depressed. The terminal area looks outwards (fig. 6 *h*), is very oblique, and not half as long as the depth of the cerci; the surface on the opposite side rather short, with about six lines. The apical seta is very short, much shorter than the area.

Length.—The adult specimens measure from 2 to 2.6 mm.

Locality.—Southern Brazils: Bella Vista (Paraná), two specimens. Paraguay: Tacurù Pucù (Alto Paraná), July 6th, 1900, two specimens. Argentina (Misiones): Pampa Piray, July 21st, 1900, one specimen; S. Ana, July 27th, 1900, two specimens; Posadas, June, 1900, four specimens. (All specimens collected by Dr. F. Silvestri.)

Remarks.—This species is easily separated from all other

forms of this group by the very thick plumose setæ on the antennæ, which, besides, typically possess a higher number of joints than in any other species of the genus. In the setæ on the posterior legs it agrees essentially with *S. vulgaris* and allied forms, but it is widely separated from them by the shape and clothing of the cerci.

EXPLANATION OF PLATES 1—7,

Illustrating Mr. H. J. Hansen's paper on "The Genera and Species of the Order Symphyla."

PLATE I.

FIG. 1.—*Scutigera immaculata* (Newp.), from Europe.

Fig. 1 *a*.—Appendages of the mouth, cleaned with caustic potash, from below. $\times 61$. The mandible on the right side of the figure omitted. *a*. Proximal joint of the mandible. *b*. Basal part of a muscle to the proximal joint. *c*. Distal joint of the mandible. *d*. Tendon to the distal joint. *e*. Maxilla. *f*. Maxillary palpus. *g*. Sternum of the segment bearing the labium. *h*. Basal joint of the labium. *i*. Second joint of the labium. *k*. Two pairs of lobes on the labium. *l*. Lateral skeleton of the head.

Fig. 1 *b*.—Distal joint of the right mandible, from above. $\times 160$.

Fig. 1 *c*.—A small part of the cutting edge of the same mandible with its "lacinia mobilis," *l*. $\times 375$.

Fig. 1 *d*.—Inner chitinous plates, *p*, of the head, the hypopharynx, *h*, and the maxillulæ, *m*, seen from above. $\times 61$.

Fig. 1 *e*.—The hypopharynx, *h*, and the maxillulæ, *m*, from above. $\times 190$.

Fig. 1 *f*.—The process containing the calicle with the tactile hair, seen from the outer side. $\times 200$. *t*. Basal part of the tactile hair.

Fig. 1 *g*.—One of the setæ from the margin of the calicle shown in Fig. 1 *f*. $\times 400$.

Fig. 1 *h*.—The same calicle with the basal parts of the tactile seta. $\times 400$.

Fig. 1 *i*.—The twenty-fifth joint of an antenna with fifty joints of a specimen from Rome, seen from the outer side. $\times 90$.

Fig. 1 *k*.—Second scutum of a large specimen from Rome. $\times 36$.

Fig. 1 *l*.—The two last scuta of the same specimen. $\times 36$. *c*. The cavity on the last scutum.

Fig. 1 *m*.—Twelfth left leg of a large specimen from Denmark, seen from in front. $\times 57$.

Fig. 1 *n*.—Claws of the twelfth right leg of the same animal, from behind. $\times 346$.

Fig. 1 *o*.—First leg of the same Danish specimen. $\times 57$.

Fig. 1 *p*.—Claws of the first right leg of the same animal, from behind. $\times 346$.

Fig. 1 *q*.—Left cercus of the same Danish animal, from the outer side. $\times 57$.

Fig. 1 *r*.—Twelfth left leg, not quite full-grown, of a specimen measuring 2.8 mm. in length from Marburg, from in front. $\times 89$.

Fig. 1 *s*.—Claws of the twelfth right leg of the same specimen, from behind. $\times 383$.

Fig. 1 *t*.—Eleventh left leg of the same specimen from Marburg, from in front. $\times 89$.

Fig. 1 *u*.—Claws on the first leg of the same specimen. $\times 383$.

Fig. 1 *v*.—Left cercus of the same small specimen from Marburg, from the outer side. $\times 89$.

FIG. 2.—*Scutigerella immaculata* (Newp.), from Buenos Aires.

Fig. 2 *a*.—Claws of the twelfth right leg of a specimen 5.4 mm. in length, from behind. $\times 400$.

Fig. 2 *b*.—Claws of the first right leg of the same large specimen, from behind. $\times 400$.

Fig. 2 *c*.—Twelfth left leg of a specimen measuring 3.5 mm., from in front. $\times 83$.

Fig. 2 *d*.—Claws of the twelfth right leg of the same smaller specimen, from behind. $\times 400$.

Fig. 2 *e*.—Claws of the first right leg of the same smaller specimen, from behind. $\times 400$.

Fig. 2 *f*.—Left cercus of the same smaller specimen, from the outer side. $\times 83$. The apical seta has been broken off.

FIG. 3.—*Scutigerella immaculata* (Newp.), from Austin, Texas.

Fig. 3 *a*.—Claws of the twelfth right leg of a large specimen 5.7 mm. in length, from behind. $\times 405$.

Fig. 3 *b*.—Claws of the first right leg of the same large specimen, from behind. $\times 405$.

Fig. 3 *c*.—Left cercus of the same large specimen, from the outer side. $\times 78$. The apical seta has been broken off.

Fig. 3 *d*.—Twelfth left leg of a smaller specimen, from in front. $\times 91$.

Fig. 3 *e*.—Claws of the twelfth right leg of the same smaller specimen, from behind. $\times 405$.

Fig. 3 *f*.—First leg of the same smaller specimen. $\times 91$.

Fig. 3 *g*.—Claws of the first right leg of the same smaller specimen, from behind. $\times 405$.

Fig. 3 *h*.—Left cercus of the same smaller specimen, from the outer side. $\times 91$.

PLATE 2.

FIG. 1.—*ScutigereUa armata*, n. sp.

Fig. 1 *a*.—Twelfth left leg, from in front. $\times 85$.

Fig. 1 *b*.—Claws of the twelfth right leg, from behind. $\times 340$.

Fig. 1 *c*.—First leg of the same specimen. $\times 85$.

Fig. 1 *d*.—Femur of the leg shown in Fig. 1 *c*, from in front. $\times 175$.

Fig. 1 *e*.—Process of the femur of another specimen. $\times 175$.

Fig. 1 *f*.—Claws of the first right leg, from behind. $\times 340$.

FIG. 2.—*ScutigereUa unguiculata*, n. sp.

Fig. 2 *a*.—The middle (sixteenth) joint of an antenna, from the outer side. $\times 180$. *s*. Small striped sense-organ.

Fig. 2 *b*.—Terminal antennal joint, from the outer side. $\times 187$.

Fig. 2 *c*.—The striped sense-organ, sitting on its protuberance, of the same terminal joint. $\times 320$.

Fig. 2 *d*.—Second scutum. $\times 52$.

Fig. 2 *e*.—Twelfth and thirteenth scuta. $\times 52$.

Fig. 2 *f*.—Twelfth left leg, from in front. $\times 68$.

Fig. 2 *g*.—Claws of the twelfth right leg of the same animal, from behind. $\times 336$.

Fig. 2 *h*.—First leg of the same specimen. $\times 68$.

Fig. 2 *i*.—Claws of the first right leg, from behind. $\times 336$.

Fig. 2 *k*.—Left cercus of the same specimen, seen from the outer side. $\times 68$.

Fig. 3.—*ScutigereUa caldaria*, n. sp.

Fig. 3 *a*.—Thirteenth joint of an antenna with twenty-five joints, from the outer side. $\times 131$.

Fig. 3 *b*.—Second scutum. $\times 58$.

Fig. 3 *c*.—Twelfth left leg, from in front. $\times 90$.

Fig. 3 *d*.—Claws of the twelfth right leg of the same specimen, from behind. $\times 415$.

Fig. 3 *e*.—Claws of the first right leg of the same specimen, from behind. $\times 415$.

Fig. 3 *f*.—Left cercus of the same specimen, from the outer side. $\times 90$.

Fig. 3 *g*.—The process with the calicle containing the tactile seta, seen somewhat obliquely and from the outer side. $\times 340$.

FIG. 4.—*ScutigereUa orientalis*, n. sp.

Fig. 4 *a*.—Twelfth left leg of a large specimen (5 mm. long) from Sumatra, from in front. $\times 60$.

Fig. 4 *b*.—Claws of the twelfth right leg of the same large specimen, from behind. $\times 275$.

Fig. 4 *c*.—First leg of the same large specimen. $\times 60$.

Fig. 4 *d*.—Claws of the first right leg of the same large specimen, from behind. $\times 275$.

Fig. 4 *e*.—Twelfth left leg of a smaller specimen from Koh Chang, from in front. $\times 76$.

Fig. 4 *f*.—Claws of the twelfth right leg of the last-named specimen, from behind. $\times 344$.

Fig. 4 *g*.—Claws of the first left leg of the last-named specimen, from in front. $\times 344$.

PLATE 3.

FIG. 1.—*ScutigereUa orientalis*, n. sp. (continued).

Fig. 1 *a*.—Head of a specimen from Koh Chang, from above. $\times 43$.

Fig. 1 *b*.—Basal part of the left antenna of the same specimen, from above. $\times 90$.

Fig. 1 *c*.—The twenty-first joint of an antenna with forty joints of a large specimen from Sumatra, from the outer side. $\times 140$.

Fig. 1 *d*.—Second scutum of a specimen from Sumatra. $\times 44$.

Fig. 1 *e*.—Penultimate scutum of the last-named specimen. $\times 44$.

Fig. 1 *f*.—Left cercus of a specimen from Koh Chang, from the outer side. $\times 76$.

FIG. 2.—*ScutigereUa plebeia*, n. sp.

Fig. 2 *a*.—Tenth left leg, from in front. $\times 86$.

Fig. 2 *b*.—Claws of the last-named leg, from in front. $\times 290$.

Fig. 2 *c*.—Claws of one of the first legs. $\times 290$.

Fig. 2 *d*.—Right cercus, seen from the outer side. $\times 86$. The apical seta has been broken off.

FIG. 3.—*Scutigera nivea* (Scop.).

Fig. 3 *a*.—Second scutum. $\times 88$.

Fig. 3 *b*.—Thirteenth scutum. $\times 88$.

Fig. 3 *c*.—Twelfth left leg of a rather small specimen, from in front. $\times 165$.

Fig. 3 *d*.—Claws of the twelfth right leg of the last-named specimen, from behind. $\times 480$.

Fig. 3 *e*.—Claws of the twelfth left leg of another specimen, from in front.

Fig. 3 *f*.—Claws of the first right leg, from behind. $\times 480$.

Fig. 3 *g*.—Claws of the first right leg of another specimen, from behind.

Fig. 3 *h*.—Left cercus of the first-named specimen, from the outer side. $\times 165$.

FIG. 4.—*Scutigera chilensis*, n. sp.

Fig. 4 *a*.—Second scutum. $\times 44$.

Fig. 4 *b*.—Thirteenth scutum of the same specimen. $\times 44$.

Fig. 4 *c*.—Twelfth left leg, from in front. $\times 82$.

Fig. 4 *d*.—Distal part of the tarsus with the claws of the twelfth right leg of the same specimen, from behind. $\times 340$. In the interior of the tarsus the claws to be used after the next moult are to be seen.

Fig. 4 *e*.—First leg of the same specimen. $\times 82$.

Fig. 4 *f*.—Claws of the first right leg of the same specimen, from behind. $\times 340$.

Fig. 4 *g*.—Left cercus of the same specimen, seen from the outer side. $\times 82$. The apical seta has been broken off.

FIG. 5.—*Scutigera capensis*, n. sp.

Fig. 5 *a*.—Twelfth left leg of the largest specimen, from in front. $\times 42$.

Fig. 5 *b*.—Claws of the last-named leg, from in front. $\times 224$.

Fig. 5 *c*.—Tenth left leg of the same specimen, from in front. $\times 42$.

Fig. 5 *d*.—Claws of the last-named tenth leg, from in front. $\times 224$.

Fig. 5 *e*.—First left leg of the same specimen, from in front. $\times 42$.

Fig. 5 *f*.—Claws of the last-named first leg, from in front. $\times 224$.

PLATE 4.

FIG. 1.—*Scutigera capensis*, n. sp. (continued).

Fig. 1 *a*.—The twenty-sixth joint of the antenna of the largest specimen, seen from the outer side. $\times 123$.

Fig. 1 *b*.—Second scutum of the largest specimen. $\times 32$.

Fig. 1 *c*.—Thirteenth scutum of the same specimen. $\times 32$.

Fig. 1 *d*.—Left cercus of the largest specimen, from the outer side. $\times 42$. The apical seta broken off.

Fig. 1 *e*.—Left cercus of the small specimen with the full number of legs, from the outer side. $\times 92$.

FIG. 2.—*Scutigerella angulosa*, n. sp.

Fig. 2 *a*.—Proximal part of the left antenna, from above. $\times 85$.

Fig. 2 *b*.—Terminal part of the last joint of the left antenna, seen from the outer side. $\times 330$. *a*. Large striped sense-organ. *b*. Small sense-organ with the stripes rudimentary. *c*. Sensory rods.

Fig. 2 *c*.—Second scutum. $\times 50$.

Fig. 2 *d*.—Thirteenth scutum of the same animal. $\times 50$.

Fig. 2 *e*.—Twelfth left leg of a very large specimen, from in front. $\times 86$.

Fig. 2 *f*.—Claws of the leg shown in Fig. 2 *e*, from in front. $\times 350$.

Fig. 2 *g*.—Twelfth left leg of a moderately large specimen, from in front. $\times 86$.

Fig. 2 *h*.—Claws from one of the first legs of a large specimen. $\times 350$.

Fig. 2 *i*.—Left cercus of the moderately large specimen (comp. Fig. 2 *g*), seen from the outer side. $\times 86$.

Fig. 2 *k*.—Eleventh left leg of a specimen with eleven pairs from Posadas, seen from in front. $\times 89$.

FIG. 3.—*Scutigerella angulosa*, var. *brevicornis*, n. var.

Fig. 3 *a*.—The eighth joint of an antenna with fifteen joints, seen from the outer side. $\times 164$.

Fig. 3 *b*.—Distal part of the terminal joint of an antenna, with various organs, from the outer side. $\times 330$.

Fig. 3 *c*.—Second scutum. $\times 59$.

Fig. 3 *d*.—Thirteenth scutum. $\times 59$.

Fig. 3 *e*.—Twelfth left leg, from in front. $\times 120$.

Fig. 3 *f*.—Claws of the twelfth left leg of the same specimen, from behind. $\times 480$.

Fig. 3 *g*.—Claws of the first right leg of the same specimen, from behind. $\times 480$.

Fig. 3 *h*.—Left cercus of the same specimen, seen from the outer side. $\times 120$.

FIG. 4.—*Scutigerella crassicornis*, n. sp.

Fig. 4 *a*.—Proximal part of the left antenna of a large specimen, seen from the outer side. $\times 40$.

Fig. 4 *b*.—The eight proximal joints of the left antenna of a large specimen, from above. $\times 80$.

Fig. 4 *c*.—Left cercus, from the outer side. $\times 88$.

PLATE 5.

FIG. 1.—*ScutigereUa crassicornis*, n. sp. (continued).Fig. 1 *a*.—Head, from above. $\times 52$.Fig. 1 *b*.—The sixteenth joint of a left antenna with thirty-one joints, seen from the outer side. $\times 131$. *t*. Sensory rod.Fig. 1 *c*.—Second scutum. $\times 55$.Fig. 1 *d*.—Twelfth left leg, from in front. $\times 88$.Fig. 1 *e*.—Claws of the twelfth right leg, from behind. $\times 330$.Fig. 1 *f*.—First leg. $\times 88$.Fig. 1 *g*.—Claws of the first right leg, from behind. $\times 330$.FIG. 2.—*ScutigereUa pauperata*, n. sp.Fig. 2 *a*.—The thirteenth joint of an antenna with twenty-seven joints, seen from the outer side. $\times 200$.Fig. 2 *b*.—Terminal joint of an antenna, seen from the outer side. $\times 200$.Fig. 2 *c*.—Distal sense-organs on the joint shown in Fig. 2 *b*, strongly magnified.Fig. 2 *d*.—Second scutum. $\times 80$.Fig. 2 *e*.—Twelfth left leg of a well-developed specimen, from in front. $\times 130$.Fig. 2 *f*.—Claws of the twelfth right leg of the same specimen, from behind. $\times 400$.Fig. 2 *g*.—Leg of the first pair of the last-named specimen. $\times 130$.Fig. 2 *h*.—Claws of the first right leg of the same specimen, from behind. $\times 400$.Fig. 2 *i*.—Left cercus of the same specimen, seen from the outer side. $\times 130$.FIG. 3.—*Scolopendrella notacantha*, Gervais.Fig. 3 *a*.—Head, from above. $\times 56$.Fig. 3 *b*.—Twelfth joint of an antenna, seen from the outer side. $\times 200$.Fig. 3 *c*.—Second scutum. $\times 84$.Fig. 3 *d*.—Posterior part of the twelfth scutum. $\times 84$.Fig. 3 *e*.—Eleventh left leg, from in front. $\times 165$.Fig. 3 *f*.—Claws of the eleventh right leg of the same specimen, from behind. $\times 450$.Fig. 3 *g*.—First leg of the same specimen, from behind. $\times 165$.Fig. 3 *h*.—Claws of the first right leg of the same specimen, from behind. $\times 450$.Fig. 3 *i*.—Left cercus of the specimen mentioned, seen from the outer side. $\times 165$.Fig. 3 *k*.—The terminal area of the cercus, seen obliquely from the outer

side and from above. $\times 370$. Only the basal part of the apical seta has been drawn.

FIG. 4.—*Scolopendrella microcolpa*, Muhr.

Fig. 4 *a*.—Head, from above. $\times 80$.

Fig. 4 *b*.—The sixth joint of an antenna, seen from the outer side. $\times 185$.
s. One of its plumose setæ more strongly magnified.

Fig. 4 *c*.—Antepenultimate joint of the same antenna, seen from the outer side, and drawn with the same degree of enlargement as Fig. 4 *b*.

Fig. 4 *d*.—Twelfth left leg, from in front. $\times 134$.

Fig. 4 *e*.—Claws of the twelfth right leg of the same specimen, from behind. $\times 430$.

Fig. 4 *f*.—First leg of the same specimen. $\times 134$.

Fig. 4 *g*.—Claws of the first right leg of the specimens mentioned, from behind. $\times 430$.

Fig. 4 *h*.—Process containing the left calicle with the base of the tactile hair. $\times 368$.

PLATE 6.

FIG. 1.—*Scolopendrella microcolpa*, Muhr (continued).

Fig. 1 *a*.—Second and third scuta. $\times 95$.

Fig. 1 *b*.—Left cercus, from the outer side. $\times 134$.

FIG. 2.—*Scolopendrella subnuda*, n. sp.

Fig. 2 *a*.—Twelfth joint of an antenna with twenty joints, seen from the outer side. $\times 350$.

Fig. 2 *b*.—Second and third scuta. $\times 148$.

Fig. 2 *c*.—Twelfth left leg, from in front. $\times 250$.

Fig. 2 *d*.—Claws of the leg shown in Fig. 2 *c*, from in front. $\times 500$.

Fig. 2 *e*.—First leg of the same specimen. $\times 250$.

Fig. 2 *f*.—Claws of the leg shown in the preceding figure. $\times 500$.

Fig. 2 *g*.—Left cercus of the same specimen, seen from the outer side. $\times 250$.

FIG. 3.—*Scolopendrella Silvestrii*, n. sp.

Fig. 3 *a*.—Sixth joint of an antenna, seen from the outer side. $\times 260$.

Fig. 3 *b*.—The second scutum and the processes of the first scutum. $\times 170$.

Fig. 3 *c*.—Eleventh left leg, from in front. $\times 200$.

Fig. 3 *d*.—Claws of the leg shown in Fig. 3 *c*, from in front. $\times 460$.

Fig. 3 *e*.—First leg of the same specimen. $\times 200$.

Fig. 3 *f*.—Tarsus with one claw—the other hidden behind—of one of the first pair of legs. $\times 460$.

Fig. 3 *g*.—Left cercus of the same specimen, seen from the outer side. $\times 200$.

FIG. 4.—*Scolopendrella Isabellæ*, Grassi.

Fig. 4 *a*.—The ninth antennal joint, seen from the outer side. $\times 190$.

Fig. 4 *b*.—Second and third scuta. $\times 77$.

Fig. 4 *c*.—Twelfth left leg, from in front. $\times 127$.

Fig. 4 *d*.—Claws of the twelfth right leg of the same specimen, from behind. $\times 430$.

Fig. 4 *e*.—Left leg of the first pair, from the outer side. $\times 430$.

Fig. 4 *f*.—Left cercus of the same animal, seen from the outer side. $\times 127$.

Fig. 4 *g*.—Distal part of the same cercus, seen from the outer side, and showing the prominent dorsal and lateral lines. $\times 500$.

Fig. 4 *h*.—Distal part of a cercus seen from below, showing the stripes on the terminal area and the base of the lateral lines. $\times 500$.

FIG. 5.—*Scolopendrella texana*, n. sp.

Fig. 5 *a*.—The thirteenth joint of an antenna with nineteen joints, seen from the outer side. $\times 122$.

Fig. 5 *b*.—Second scutum. $\times 85$.

Fig. 5 *c*.—Twelfth left leg, from in front. $\times 122$.

Fig. 5 *d*.—Claws of the twelfth right leg of the same animal, from behind. $\times 416$.

Fig. 5 *e*.—Left cercus, seen from the outer side. $\times 122$. The apical seta has been broken off.

FIG. 6.—*Scolopendrella vulgaris*, n. sp.

Fig. 6 *a*.—Twelfth left leg, from in front. $\times 165$.

Fig. 6 *b*.—Claws of the twelfth right leg of the same specimen, from behind. $\times 430$.

Fig. 6 *c*.—Left leg of first pair, from the outer side. $\times 430$.

Fig. 6 *d*.—Left cercus, from the outer side. $\times 165$.

PLATE 7.

FIG. 1.—*Scolopendrella vulgaris*, n. sp. (continued).

Fig. 1 *a*.—Second and third scutum. $\times 90$.

FIG. 2.—*Scolopendrella neotropica*, n. sp.

Fig. 2 *a*.—Seventh joint of the left antenna, seen from the outer side. $\times 170$.

Fig. 2 *b*.—Second and third scuta. $\times 80$.

Fig. 2 *c*.—Twelfth left leg, from in front. $\times 133$.

Fig. 2 *d*.—Claws of the twelfth right leg of the same specimen, from behind. $\times 425$.

Fig. 2 *e*.—Claws of the second right leg of the same specimen, from behind. $\times 425$.

Fig. 2 *f*.—Left first leg, from the outer side. $\times 425$.

Fig. 2 *g*.—Left cercus of the specimen mentioned, from the outer side. $\times 133$.

FIG. 3.—*Scolopendrella simplex*, n. sp.

Fig. 3 *a*.—Second and third scuta. $\times 120$.

Fig. 3 *b*.—Twelfth left leg, from in front. $\times 152$.

Fig. 3 *c*.—Claws of the twelfth right leg of the same specimen, from behind. $\times 460$.

Fig. 3 *d*.—Left first leg, from the outer side. $\times 460$.

Fig. 3 *e*.—Left cercus of the specimen mentioned, from the outer side. $\times 152$.

FIG. 4.—*Scolopendrella pusilla*, n. sp.

Fig. 4 *a*.—Second and third scuta. $\times 131$.

Fig. 4 *b*.—Twelfth left leg, from in front. $\times 212$.

Fig. 4 *c*.—Left cercus of the same specimen, from the outer side. $\times 212$.

FIG. 5.—*Scolopendrella brevipes*, n. sp.

Fig. 5 *a*.—Second and third scuta. $\times 153$.

Fig. 5 *b*.—Twelfth left leg, from in front. $\times 200$.

Fig. 5 *c*.—First left leg, from the outer side. $\times 200$.

Fig. 5 *d*.—Left cercus of the same specimen, seen from the outer side. $\times 200$.

Fig. 5 *e*.—The same cercus, from above. $\times 200$.

FIG. 6.—*Scolopendrella antennata*, n. sp.

Fig. 6 *a*.—Eighth antennal joint, seen from the outer side. $\times 210$. *s*. One of the plumose setæ strongly magnified. The specimen is from St. Ana.

Fig. 6 *b*.—Fourth antennal joint of another specimen, from above. $\times 210$.

Fig. 6 *c*.—Twelfth antennal joint of the last-named specimen (from Bella Vista), from above. $\times 210$.

Fig. 6 *d*.—Second and third scuta of a specimen from Tacurù Pucù. $\times 120$.

Fig. 6 *e*.—Twelfth left leg of a specimen from St. Ana, from in front. $\times 146$.

Fig. 6 *f*.—Claws of the twelfth right leg of the last-named specimen, from behind. $\times 440$.

Fig. 6 *g*.—First left leg of the last-named specimen, seen from the outer side. $\times 440$.

Fig. 6 *h*.—Left cercus of the last-named specimen from St. Ana, seen from the outer side. $\times 146$.

Fig. 6 *i*.—The same cercus, from above. $\times 146$.

Postscript.—In the autumn of 1902 Dr. F. Silvestri told me in a letter that he had worked out a new treatment of the Italian species of the Symphyla and Pauropoda; it had been accepted in Berlese's work 'Acari, Myriopoda et Scorpiones huc. in Italia rep.,' and he believed that Prof. Berlese was about to distribute the part in question to the subscribers. When in the second week of December I looked over the proofs of my paper I asked for the part mentioned in the "Great Royal Library" in Copenhagen, which has purchased Berlese's work, but the library had not yet received that new part. Therefore I do not know whether it really had been published when I looked over the proofs, and I could not compare my species from Italy with those described by Dr. Silvestri.

On the Body-Cavities and Nephridia of the Actinotrocha Larva.

By

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With Plates 8 and 9.

ON a previous occasion I announced the discovery of solenocytes in the larva of *Phoronis* (8, p. 499, note 1), and the following paper contains an account of the structure and relations of its excretory organs. Since it is necessary to discuss the nature of the various cavities in the larva in order to thoroughly elucidate the morphological relations of the nephridia, I have gone into some detail on this question, and have illustrated my observations with some diagrammatic reconstructions which will, I hope, render my conclusions clear to the reader. The work is based on the examination of sections of some large *Actinotrocha* larvæ I caught at Trincomalee in 1899, and more especially on the study of some abundant material I obtained at Faro last July (1902).¹ The Cingalese larvæ are provided with about thirty-six slender tentacles; the Sicilian larvæ when full grown have fourteen tentacles, and probably belong to *Phoronis psammophila*.

¹ I gladly take this opportunity of thanking Professor Dohrn for the loan of apparatus to equip an expedition I undertook from the Zoological Station at Naples, with my friend Dr. Shearer.

Few new points are presented in this paper, the work having been chiefly of a critical and corroborative nature; but the results of the study of this interesting larva which have been published are so contradictory that no apology need be made for an attempt to reconcile such conflicting views.

Although the larva of *Phoronis* was discovered and described by Johannes Müller as early as 1846, and several zoologists have studied it since, many points in its anatomy and development remain still but imperfectly known.

The literature on the subject has been so well and so recently analysed by Masterman (11), de Selys Longchamps (16), and Ikeda (9), that it is only necessary for me to refer to those writings of previous authors which deal more particularly with the body-cavities and nephridia.¹

The earlier observers gained a good general knowledge of the external features of various stages, of the chief events in the metamorphosis, and of the general internal anatomy of *Actinotrocha* (Müller [15], Wagener [18], Krohn [10], Schneider [17], Claparède [4], Metschnikoff [14], Gegenbaur [5]). But to Caldwell belongs the credit of first presenting, in 1882 (2), a clear account of the details of the internal anatomy and of the internal changes undergone during metamorphosis. Unfortunately Caldwell's paper was not accompanied by adequate figures. Nevertheless his observations were so accurate and so detailed, and his interpretation of the morphology of the larva was in the main so good, that his successors have done little but corroborate, extend, and, in some respects, correct his results.

THE CAVITIES.

According to Caldwell (2) there are in the *Actinotrocha* larva two main cavities, separated by a complete septum;

¹ Roule's results differ so fundamentally from those of other writers and from my own that it seems safer not to criticise his work without having studied the species he examined ('Ann. des Sci. Zoologie,' vol. xi, 1900).

also the rudiments of a dorsal vessel and a vascular space round the stomach, which arise as "splits in the splanchnopleure." "The septum," says Caldwell, "is attached in a circle along the line of the nerve-ring [at the base of the tentacles], and free communication exists between the body-cavity in front of the septum and the split in the splanchnopleure, which will form the blood sinus and vessels of the adult." He found a ventral mesentery extending from the septum to the anus. "The blood-corpuscles . . . arise from the mesoblast cells in front of the septum." As we shall see, this description is in the main correct, and Caldwell failed only in that he did not observe a separate cœlomic cavity in front of the septum.

Since Caldwell, Masterman published, in 1898, a paper on *Actinotrocha* (11), in which many alleged new features are described; K. Ramunni Menon has contributed some notes on an Indian species (13); de Selys Longchamps has discussed the development and structure of certain European forms (16); whilst Iwaji Ikeda has brought forth a most valuable paper on the larval history of *P. iijimai* from Japan (9).

Masterman appears to have been so strongly influenced by theoretical prejudices in his interpretations of the structure of the larva that his account cannot be accepted as trustworthy. Of the several important new points described by this author the following may be mentioned:—The presence of two "proboscis pores:" "on either side of the middle line, near the nerve-ganglion, a pore leads by a short canal into the cœlomic cavity of the pre-oral lobe." The "neuropore:" "a long sac-like diverticulum lying under the nerve-ganglion." The notochord-like character of the gastric cæcum. The "subneural gland:" a diverticulum of the cesophagus projecting inwards below the brain. The "subneural sinus:" "there is just under the nerve-ganglion a large sinus caused by a want of continuity between the mesoblastic walls of the pre-oral cavity in front and the collar cavities behind. . . . At the posterior end of the

sinus it leads by a chink or fissure between the gut wall and that of the two collar cavities along the dorsal wall of the œsophagus to the hind extremity of the collar region. Here it falls into the large dorsal vessel with contractile walls." The anterior septum: a "well-marked mesentery" separating the "collar cavity" from the cavity of the pre-oral lobe. A dorsal mesentery and a dorsal vessel in the "collar" region. The termination of the nephridia by "broad funnels," which, "without doubt, open into the collar cavities." Masterman's successors have already dealt severely with these contributions to our knowledge of the anatomy of *Actinotrocha*.

Ikeda (9) is "much inclined to regard the 'neuropore' of Masterman not as a really existing structure, but as an artefact." De Selys Longchamps is also unable to discover evidence of its existence (16), and Menon can only find a depression lying "in the actual ganglion" (13). My observations strongly uphold the opinion of Ikeda. Artificial "sac-like" depressions I have frequently found in front of the ganglion in specimens in which the pre-oral lobe had been turned upwards during fixation by the reagents. The ganglion is bilobed dorsally, and between the two hinder diverging lobes may be generally noticed a very slight depression surrounded by elongated cells from which spring a tuft of very long cilia. This slight pitting, which may or may not be artificial, is comparable to the similar flattening or depressing of the surface seen in the apical region of trochosphere larvæ.

The existence of a "subneural gland" has been denied by Ikeda (9). Menon and de Selys Longchamps (13 and 16) describe slight depressions above the mouth. My own observations entirely confirm the opinion of Ikeda that this folding of the œsophageal wall is mainly a product of the fixing method.

The stomach of *Actinotrocha* bulges forwards below the narrow œsophagus so as to give rise to a ventral diverticulum. In some species, such as *Actinotrocha branchiata*, this diverticulum bifurcates in front so as to project on either

side of the œsophagus, as described by Müller, Wagener, and others. The wall of the ventral outgrowth differs but slightly in histological structure from that of the remainder of the ventral wall of the stomach; but its granular cells are generally vacuolated, large droplets of fatty-looking fluid being situated at their outer ends (figs. 4, 13). Masterman has compared this gastric cæcum of *Actinotrocha* to the notochord of Vertebrates. The two organs seem to me fundamentally different both in their relations and in their histological structure; and I agree with Menon, Ikeda, and de Selys Longchamps that Masterman's theory as to its homology is quite unjustified. I may repeat the statement of Longchamps that the histological characters of the gastric cæcum "*sont absolument différents de tout ce qui a jamais été observé dans une notochorde quelconque*" (16).

We may now turn to those structures with which we are more directly concerned—the cavities themselves.

It is generally agreed, since the appearance of Caldwell's paper, that there exists in the trunk region of the larva, behind the ring of tentacles, a large cœlomic cavity in which the gut lies attached to the body-wall by a median ventral mesentery. It is in this cavity that the ventral pouch grows, carrying the mesentery with it. This trunk cavity is limited in front by a definite complete septum, which has an oblique course, being attached much further forward dorsally than ventrally. Concerning the posterior limits of the trunk cœlom there is some disagreement. Masterman described a perianal sinus on the inner side of the perianal ciliated ring, and added that "at the perianal area are a pair of organs which I have not fully made out, but they may be the rudiments of the trunk nephridia. They lie in the hæmocoel space immediately below the ciliated band, and are thin walled. They have an internal opening into the trunk cœlom, and apparently open to the exterior on either side of the anus. Their walls are of the same nature as those of the cœlom, and appear to be portions of the cœlom, with the trunk nephridial tubes cut off from the rest of the trunk

cœlom." From this description the relations of the problematic organs are by no means easy to understand, and the author himself seems to be very doubtful as to their existence (11 and 12). Ikeda looks upon the perianal sinus as a purely artificial space. This, indeed, may be the case in some species, as, for instance, in the larva I obtained in Ceylon. In this *Actinotrocha* (fig. 9) the cœlomic epithelium is separated in the perianal region from the outer body-wall only for a short distance above and below the thick ciliated ring. The chink between the two layers contains no clear space at all, but appears to be filled up with a connective tissue of fine mesoblastic fibres—possibly coagulation products in a jelly-like substance.

Menon (13) has described a perianal sinus, and de Selys Longchamps appears to have found a similar space in his species (16). Such a cavity certainly seems to exist in the species from Faro (fig. 1, *pa.s.*) when the perianal band is expanded; but when it is withdrawn together with the anus (as it frequently is), so that the cilia point inwards into a temporary posterior depression, the cœlomic epithelium is stretched tightly over the inner surface of the ciliated ring, and the cavity then vanishes almost completely. The looseness of the cœlomic epithelium in this region, in fact, appears to be only a device whereby the invagination of the perianal ciliated ring can be brought about. The thin posterior septum, with radiating and probably contractile bands (fig. 1), forms a complete membrane shutting off the perianal sinus. It is not formed of separate "brides mésentériques," as suggested by de Selys Longchamps (16).

The problematic posterior trunk nephridia have been severely dealt with by Menon and Ikeda (13 and 9); I need only add that my own observations entirely support their view and Masterman's own recent statement that "it would be as well to state once for all that the trunk has no nephridia and possesses no normal openings till after the metamorphosis" (12).

There is much less agreement concerning the cavities in

front of the main septum. Basing his nomenclature on a comparison with *Balanoglossus* and *Cephalodiscus*, Masterman (11) speaks of two distinct coelomic cavities—an anterior pre-oral coelom in the hood and a larger coelomic cavity, which he calls the “collar” cavity, separated from the first by a complete septum below the brain, and reaching back to the main and more posterior septum. Whilst, according to this author, the “collar” coelom communicates with the exterior by means of the two nephridia, the pre-oral coelom is said to open to the exterior by two “proboscis pores,” one on each side of the ganglion. Moreover a separate “sub-neural sinus” is supposed to exist, lying between the two layers of the anterior septum, and to communicate with the longitudinal dorsal blood-vessel.

Now Caldwell (2) describes only the single main septum separating a trunk coelom from a pre-septal blood-cavity in front, occupying both the hood and the region behind it, and continued backwards into the longitudinal blood-vessel. This single extensive cavity may be called the “pre-septal cavity,” to avoid all morphological prejudice. Menon (13), de Selys Longchamps (16), and Ikeda (9), all three deny the existence of “proboscis pores.” I have no hesitation in saying that no such pores exist in any larvæ I have examined, whether from *Faro* or from *Trincomalee*.

Menon, on the other hand, appears to confirm Masterman's statement as to the existence of a complete septum separating a “pre-oral” from a “collar” cavity; but his account is inadequately illustrated, and by no means convincing. Whilst the alleged septum is said to be attached just behind the nerve-ganglion, it is drawn (Pl. 26, fig. 6) in a position well behind the hood itself. The “pre-oral” cavity is said to contain “scattered blood-corpuscles and coelomic corpuscles,” and to be of a nature “which it is thus difficult to decide.” There is reason to believe that Menon has, moreover, confused the true pre-septal coelom (c. c. in his figures 2, 3, and 4) with the pre-septal hæmocoel (c. c. in his figures 5, 6, and 8). According to Menon the “subneural

sinus" is "a completely closed vesicle" with an internal lining of distinct epithelium (13).

De Selys Longchamps (16), on the contrary, denies the existence of a complete anterior septum. He finds "des formations mésenchymatiques . . . particulièrement développées entre le ganglion nerveux central et le 'subneural gland' . . . constituent en ce point une membrane, rattachant la paroi dorsale du lobe préoral à la paroi de l'œsophage . . . il n'y a pas, pour cela, séparation entre les deux cavités." Further, he rightly insists that there is a single hæmal pre-septal cavity: "Dans la cavité antérieure, commune au lobe préoral et à la région collaire, un mésenchyme surtout abondant dans la première de ces deux régions; dans la cavité postérieure du corps, un mésoderme épithélial, représenté par une splanchnopleure et une somatopleure, et un mésentère sous-intestinal typique." In fact, the Belgian observer confirms Caldwell's account.

Ikeda's statements, accompanied by elaborate figures, are even more convincing (9). He shows that muscular strands pass from the sides of the ganglion to the œsophagus and to the body-wall, that a membrane stretches across these muscles, forming the dorsal limit of a "posterior recess" of the pre-oral region. This recess is a sort of pocket bulging backwards beneath the brain. It opens forwards into the spaces of the pre-oral hood, which communicate widely with the main space in the "collar" region. Blood-corpuscles may be found in all these spaces, and they are of a hæmocœlic nature.

My own results entirely confirm those of Ikeda on this question of the anterior septum. A subneural pocket is present (figs. 1, 4, 12, and 9); it is lined with a conspicuous epithelium, and when seen in frontal sections may present the appearance of being a completely closed cavity (fig. 12). But, as I have endeavoured to show in figures 1 and 9, the pocket is widely open ventrally, and its cavity is merely a portion of the general pre-septal cavity. It is this clear space which allows of the ganglion being withdrawn by the muscles

already alluded to above. The remainder of the hood-cavity is for the most part occupied by a more or less dense mass of delicate fibres, with occasional nucleated mesenchymatous cells. The presence of the fibres may be to some extent due to the coagulating action of the fixative.

As already stated by Ikeda, with regard to *Phoronis iijimai*, neither dorsal vessel nor dorsal mesentery exists in the pre-septal "collar" region of the larva. It is difficult, indeed, to see how these structures, described by Masterman, could be present, since the pre-septal cavity is itself a part of the blood-system, containing blood-corpuseles, and giving rise in later stages to the lophophoral blood-vessel.

There remains to describe the true pre-septal coelom. Strangely enough Ikeda is the first and only author who has given a correct account of this cavity (9). "The adult collar cavity, or the supra-septal cavity," says Ikeda, "is already formed in the fully developed larva of every type as a ring space running along the inner side of the tentacular circle and above the septum." He further shows that this ring-like rudiment of the adult pre-septal coelom sends out a caecum into the base of each tentacle. Ikeda gives no details as to the origin of the pre-septal coelom, nor have I been able to follow it for certain myself. It makes its appearance somewhat late in larval life, when the ventral sac is already well formed, as a split between two layers of a narrow band of mesoblast adhering closely to the body-wall just above the septum and just below the tentacles. So far as I have been able to make out the ring is never completed dorsally. An advanced larva shows a pre-septal coelom of considerable size, which runs round the base of the tentacles, sending out a blind process into each (figs. 2 and 10). It terminates dorsally in two horns, which run forwards for some little space on either side of the middle dorsal line towards the ganglion (figs. 2 and 13).

We may now attempt to give in a few words a clear description of the cavities in the *Actinotrocha* larva.

Behind the circle of tentacles there is a single trunk

cœlom, through which passes the alimentary canal, suspended by a median ventral mesentery. This cavity does not communicate with the exterior; it is limited in front by a complete septum, and behind is, in some forms, but not in all, separated from the body-wall by a perianal sinus.

In front of the septum are two distinct cavities. The larger of these is the pre-septal hæmocœl, a blood-cavity which occupies nearly the whole region from the septum to the edge of the pre-oral hood. Muscular strands and fibrous strands traverse it in many directions, and in the later stages hæmoglobinous blood-corpuscles float in the fluid contained in it. The epithelium lining this cavity is not as distinct as that of the cœlomic cavities, and in some regions is but irregularly if at all developed. A distinct pocket, with an epithelial lining, is situated between the brain and the œsophagus, and opens ventrally. The subneural space is but a portion of the general pre-septal hæmocœl. Continuations of the pre-septal hæmocœl extend to the tips of the tentacles and down the mid-dorsal and the mid-ventral lines, forming the blood-vessels lying on the stomach. During metamorphosis it becomes converted into the ring or lophophoral blood-vessel of the adult.

Running close beneath the body-wall anteriorly to the septum is the pre-septal cœlom. This cœlomic space is in the form of a horseshoe-shaped canal, sending a short blind branch into the base of each tentacle. It appears somewhat late, and becomes converted into the pre-septal or lophophoral cœlom of the adult. Neither of the pre-septal cavities open to the exterior in the larva.

We are now in a position to discuss the structure and relations of the nephridium itself.

THE NEPHRIDIA.

Wagener, in 1847 (18), was the first to describe the excretory organs of *Actinotrocha*, and his figure of the nephridium, with its bunch of elongated "spermatozoon-like

cells," remains the best yet published. Caldwell (2) added greatly to our knowledge of the structure and development of these organs. "The nephridium," he writes, "is a ciliated canal with cellular walls. The canal is not formed of perforated cells. . . . Each canal opens to the exterior behind the septum on either side of the opening of the foot. The canal lies outside the somatic mesoblast" (the lining of the trunk cœlom). "Attached to its inner end," he adds, "are cells of very peculiar form. Each cell has a nucleus and processes similar to those of ordinary mesoblast cells. By one of these the cell is attached to the end of the large canal. This process is larger than the free processes, and has a cylindrical form. By the canal formed inside the cylinder small brown concretions seen in the cell itself pass into the large canal, and so to the exterior. These excretory cells, with their fine canals, increase in number with the growth of the larva. They float freely in the body-cavity in front of the septum." "The cells are similar to the perforated cells which form the internal ends of the nephridia described by Hatschek in *Echiurus*." "At no time during the free-swimming life of [the] larva does the excretory canal system open into the body-cavity."

None of the authors who succeeded Caldwell have given such an accurate account of the structure of the nephridium. De Selys Longchamps merely confirms his statement that it does not open into the pre-septal hæmocœl. Ikeda (9) comes to the same conclusion, and describes "spindle-shaped excretory cells" on the blind internal extremity, and an epithelium covering the nephridial tube.

Masterman, on the other hand, led astray by the desire to compare the nephridium of *Actinotrocha* with that of *Amphioxus* as described by Boveri, considers that it opens by several funnels into the pre-septal cavity, which he mistook for cœlom. As pointed out by Ikeda, Masterman confused the mass of blood-corpuscles with the "excretory cells" of Caldwell: "a pair of large bodies, apparently aggregations of amœboid cells, with large nuclei. . . . The cells are

grouped round a few intercellular canals, which open into the collar cavity by broad funnels. . . . The internal funnels, without doubt open into the collar cavities" (11).

Menon, who gives a more correct figure of the excretory cells, has likewise described internal openings to the nephridia (13).

A careful study of the nephridia of *Actinotrocha* in the living, in teased preparations, and in sections has convinced me that no such opening exists. The nephridial canal is intercellular, has a narrow ciliated lumen, and opens by a small external pore on the ventral surface some distance behind the ring of tentacles. It passes forwards and inwards between the cœlomic epithelium of the trunk cavity and that of the pre-septal cœlom (when the latter is developed) until it reaches the anterior surface of the septum, and projects freely into the large pre-septal blood space (figs. 5, 2, and 10). This projecting portion of the nephridium does not appear to be externally covered by a regular epithelium. The extreme inner end of the nephridial canal expands considerably, while its wall thins out into a mere membrane. It is this expanded region which has been mistaken for an open funnel. On the thin wall of the terminal expansion are situated the excretory cells, which are, in fact, typical solenocytes.

Figs. 5, 6, 7, 8, and 15 illustrate the structure of the solenocytes in the larvæ from Faro. The cell-body is provided with long, protoplasmic, free processes similar to those I have described in *Nephthys* and other *Polychætes* (6). The nucleus is bent round so as to embrace the extremity of the tube (figs. 7 and 8). Owing to this curved shape of the nucleus the solenocytes often present the deceptive appearance of possessing two or three small nuclei. The tube itself, which is of a cuticular substance, staining blue with nigrosin, is somewhat short and wide. It does not project into the lumen of the nephridial canal as in the case of *Amphioxus* and many *Polychætes* (6 and 8). A certain quantity of protoplasm seems to extend down the tube from the cell-body on the side on which the nucleus is situated. A long flagellum is

attached at the free end of the tube, near the nucleus, and passes down the tube into the nephridial canal. In the case of the larger *Actinotrocha* from Trincomalee, the nephridium gives off two or three short branches at its inner end, on which are placed a very large number of solenocytes. The nucleus is more spherical, but in other respects the solenocytes differ but very slightly from those of the Sicilian larvæ.

Caldwell's description, then, appears to be quite accurate so far as it goes; the flagellum working inside the "cylinder" is really the only thing he missed. His comparison of the nephridia of *Actinotrocha* with the nephridium of the larva of *Echiurus* and the similar excretory system of *Platyhelminths* is most happy, and the facts supply another link in the chain of evidence in favour of the view I have long been supporting (6 and 7).

Concerning the origin of the nephridia of *Actinotrocha*, the views of previous authors are by no means in accord. It was my intention, when I first undertook this work, to trace the origin and fate of these interesting organs. Unfortunately I have not been able to obtain the necessary material for a complete history of their development. Others will, I hope, soon be able to fill the gaps in our knowledge on this important subject. Caldwell believed the nephridia to arise from the invagination at the "posterior pit." "I have observed," he says, "mesoblastic cells, at the time when the mesoblastic sacs of the trunk are forming, take the characteristic shape of excretory cells with cylindrical processes. . . . I have failed to discover the origin of the main ciliated canal. . . . Dr. Hatschek believed that the whole organ was formed from the mesoblast cells mentioned above" (2). De Selys Longchamps is uncertain as to the origin of the nephridium (16).

It is to Ikeda's excellent work that we must turn for the most complete account of its development (9). This author describes the origin of the nephridia from the invagination of the epiblast (Caldwell's mesoblast) at the "posterior pit." The invagination is said to sink inwards, to bifurcate, and

finally to become separated into two blind tubes projecting into the pre-septal hæmocœl, and opening to the exterior. "Besides," writes Ikeda, "a certain number of mesenchymatous cells, which later undoubtedly become the excretory cells of *Actinotrocha*, are always found attached to the blind ends of the nephridial canals." I feel convinced that these so-called mesenchymatous cells are the cells described by Caldwell, and really derived from the epiblastic invagination.

An accurate and detailed account of the origin of the solenocytes of *Actinotrocha* is still wanting. Should the nephridia prove to be actually developed from the epiblast, this origin and their ascertained relation to the hæmocœl would be welcomed as two more nails in the coffin of that theory according to which the nephridia are parts of the cœlom.

Another hardly less uncertain and perhaps even more important question which remains to be settled concerns the fate of these nephridia after metamorphosis.

It is well known that there are in the adult *Phoronis* two organs opening near the anus, which communicate with the post-septal trunk cœlom by means of wide open ciliated funnels. In some species, at all events, a similar opening occurs into the pre-septal cœlom—as in *Phoronis australis* (Benham [1]). These organs, generally called the nephridia, function both as excretory and as genital ducts. Now it is clear that, if they in any way represent the nephridia of the larva, they must have lost their primitive connection with the pre-septal blood-vascular ring, and have acquired new openings into the cœlomic cavities. Since it is generally agreed that no trace of a second pair of excretory organs occurs in the larva, the question we have to decide is how far the adult organs are due to new formations, and how far to the modification of the larval nephridia during or after metamorphosis.

Caldwell describes how, at metamorphosis, "the larval excretory cells of the nephridia break off from the large canal and float freely in the body-cavity in front of the septum. They pass with the blood-corpuscles into the vessels.

The large canals remain as the paired nephridia of the adult."

De Selys Longchamps is also of the opinion that the canal of the larval nephridia persists as that of the adult organs, and that "ces canaux acquièrent secondairement chacun un orifice en entonnoir qui débouche dans la cavité postérieure du corps." Menon likewise states that the larval "nephridia become the nephridia of the adult *Phoronis*," and Ikeda comes to much the same conclusion.

In just-metamorphosed larvæ from Faro I find the canal of the larval nephridium occupying just the same position on each side of the anus as the excretory ducts of the adult, and showing no signs of degeneration (fig. 3). The inner blind end still lies in the pre-septal hæmocœl (lophophoral ring vessel), but, as Caldwell observed, the solenocytes have disappeared. Their remnants are possibly to be found in certain small deeply-staining nuclei floating in the blood. No trace whatever can be seen of an opening into the cœlom at this stage, and I am strongly of the opinion that the cœlomic funnels are later developed from the cœlomic epithelium, as was suggested by de Selys Longchamps, and become subsequently grafted on to the nephridial canal. This is one of those important gaps in the history of these organs which still remains to be filled up.

If future observations show that the adult organ is made up of the nephridial canal of the larva to which a cœlomostome becomes added after the metamorphosis, the structure of the adult excretory organ of *Phoronis* would be wonderfully like that of the compound "nephromixia" I have described in certain Polychæte worms—more especially like those of the *Phyllodocidæ* (6).

SUMMARY AND CONCLUSION.

It has been shown above that in the *Actinotrocha* larva there is one complete septum separating a closed posterior trunk cœlom from an anterior pre-septal hæmocœl, which ex-

tends into the tentacles and into the pre-oral hood; that in front of the septum there is developed a second cœlomic cavity, in the form of a horseshoe-shaped canal, extending into the base of each tentacle; that the nephridia open to the exterior ventrally behind the septum, and project freely into the pre-septal blood space, where they end blindly; that this inner extremity of the nephridium is furnished with a bunch of typical solenocytes resembling those of *Polychætes* and of *Amphioxus*; that during metamorphosis the pre-septal cœlomic canal becomes the pre-septal adult cœlom, and that the pre-septal hæmocœl becomes reduced to the adult ring blood-vessel; that the nephridia lose their solenocytes and their connection with the ring vessel, and acquire new openings into the cœlomic cavities, probably by means of newly-formed cœlomostomes or peritoneal funnels; that the longitudinal blood-vessels open into the pre-septal hæmocœl; and that a perianal sinus may be developed near the anal ciliated band.

Much remains to be elucidated in the history of the nephridia; and the origin of the cavities has not yet been satisfactorily worked out. The possibility of the existence at a very early stage of a separate pre-oral cœlom, coming into secondary continuity with the pre-septal hæmocœl through the breaking down of an originally complete anterior septum, has not been perhaps entirely excluded; but, so far as I am aware, there is no evidence in favour of the view that such is the real history of the cavity of the hood.

The existence in *Actinotrocha* of a closed nephridium provided with solenocytes is an interesting and important fact, and its recognition enables us to add the *Phoronidea* to the already long list of animals (*Vertebrata*, *Annelida*, *Echiuroidea*, *Mollusca*, *Endoproctous Polyzoa*, *Nemertina*, *Rotifera*, and *Platyhelminia*) whose common ancestor must have possessed true nephridia of this nature. We may now expect to hear of the discovery of flame-cells or of solenocytes in the *Sipunculoidea* and *Ectoprocta*, which are doubtless related to *Phoronis*.

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LIST OF REFERENCE LETTERS IN PLATES 8 AND 9.

a. Anus. *ap.* Aperture of the ventral sac. *a. t. c.* Anterior extension of the trunk cœlom. *bl. c.* Blood-corpuscles. *c. s.* Cut edge of the septum. *c. tl. c.* Cut tentacular cœlom. *d. bl. v.* Dorsal blood-vessel. *d. h.* Dorsal horn of the pre-septal cœlom. *d. w.* Dorsal wall of the subneural pocket. *ep.* Epidermis. *f.* Mesenchymatous fibres. *fl.* Flagellum. *h.* Pre-oral hood. *gl.* Nerve ganglion or brain. *n.* Nucleus of the solenocyte. *neph.* Nephridium. *neph. p.* Nephridiopore. *neph. c.* Nephridial canal. *nv.* Anterior nerves to the pre-oral ring. *œs.* Œsophagus. *pa. c. r.* Perianal ciliated band. *pa. s.* Perianal sinus. *po. c. r.* Pre-oral ciliated band. *ps. c.* Pre-septal cœlom. *po. ps. h.* Pre-oral, pre-septal blood-space, or hæmocœl. *ps. h.* Pre-septal hæmocœl. *r.* Ridge of stomach wall. *s.* Septum. *sn. p.* Subneural pocket. *s. pa.* Septum closing off the perianal sinus. *st.* Stomach. *str.* Mesenchymatous strands. *t. c.* Trunk cœlom. *tt.* Tentacle. *tt. cœl.* Tentacular cœlom. *tt. h.* Tentacular hæmocœl. *tt. b.* Base of tentacle which grows into the adult tentacle. *v. c.* Vascular cæcum. *v. d.* Ventral diverticulum of the stomach. *v. s.* Ventral invaginated sac. *v. v.* Ventral blood-vessel. *w.* Wall separating the pre-septal hæmocœl from the cœlom.

EXPLANATION OF PLATES 8 AND 9.

Figs. 1—8, 10, 13—15 represent the larvæ from Faro.

Figs. 9, 11, and 12 represent a larva from Trincomalee.

FIG. 1.—Diagrammatic reconstruction of an Actinotrocha larva drawn as a solid object cut along a sagittal plane a little to the right of the middle line so as to avoid the median ventral mesentery. The pre-septal blood-cavity (*ps. h.*) is continuous with the pre-oral blood-cavity (*po. ps. h.*) round the sides of the subneural pocket (*sn. p.*). The pre-septal cœlomic canal (*ps. c.*) is seen cut through twice. The hæmocœl is continued backwards beyond the septum as a narrow slit along the mid-dorsal and the mid-ventral line of the stomach. The trunk cœlom (*t. c.*) is separated from the perianal sinus by a thin continuous epithelium.

FIG. 2.—Similar view of a larva from which a portion of the left body-wall has been removed, exposing the pre-septal blood-cavity, the pre-septal cœlomic canal with its tentacular branches, the ventral invaginated sac in the trunk cœlom, which extends dorsally, pushing the septum with it (*a. t. c.*), and the ventral mesentery. The inner blind end of the nephridium, provided with solenocytes, is seen projecting into the pre-septal blood-cavity. The external cilia are not represented.

FIG. 3.—Transverse section through the front end of a newly-metamorphosed larva, just in front of the anus. The solenocytes have disappeared, but the nephridial canals are seen to end blindly in the remains of the larval pre-septal hæmocœl, now transformed into the adult ring-vessel of the lophophore (*ps. h.*). Cam. Z. D, oc. 3.

FIG. 4.—Sagittal section through the anterior end of a larva showing the dorsal wall of the subneural pocket (*d. v.*) and the ventral diverticulum of the stomach (*d. v.*). Cam. Z. D, oc. 2.

FIG. 5.—Oblique longitudinal section of the nephridium passing through its closed inner end, from which spring the solenocytes. Cam. $\frac{1}{12}$ oil immersion, oc. 12.

FIG. 6.—Section through the extreme tip of a nephridium lying in the pre-septal hæmocœl. Below it runs the pre-septal cœlomic canal. The solenocytes are well shown. Cam. $\frac{1}{12}$ oil immersion, oc. 8.

FIG. 7.—A few solenocytes drawn from a section to show the relation of the nucleus to the tube. Cam. $\frac{1}{12}$ oil immersion, oc. 8.

FIG. 8.—Three solenocytes in transverse section. Cam. $\frac{1}{12}$ oil immersion, oc. 8.

FIG. 9.—Diagrammatic reconstruction of an Actinotrocha cut along a frontal plane passing below the gut and nephridia behind, and cut more dorsally in the upper half of the figure. The subneural pocket is seen below the brain. The œsophagus is cut transversely, two tentacles are cut longitudinally, and the pre-septal cœlom is cut across twice.

FIG. 10.—Reconstruction of an oblique section parallel to and above the septum, passing through the pre-septal cœlom. The anterior dorsal prolongation of the trunk cœlom is cut into, the œsophagus and the ventral diverticulum are cut across, and the blind ends of the nephridia are seen projecting into the pre-septal hæmocœl.

FIG. 11.—Frontal section passing through the ventral cœcum of the stomach and in front of the ganglion. Cam. Z. A, oc. 3.

FIG. 12.—Frontal section of the same series passing through the ganglion and underlying subneural pocket. Cam. Z. A, oc. 2.

FIG. 13.—Transverse section in front of the septum (compare fig. 10). Cam. Z. D, oc. 3.

FIG. 14.—Transverse section taken through the anterior region of the trunk cavity and the posterior limits of the septum. The nephridia and the ventral region of the pre-septal cœlom are cut through. Cam. Z. D, oc. 3.

FIG. 15.—Diagram of the nephridium of a young Actinotrocha showing the canal and the solenocytes.

Enteropneusta from Madras.

By

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With Plate 10.

DURING the last few months I have been able to dredge on a small scale off the Madras Coast. The specimens already obtained include a number of interesting forms, and I was especially gratified to find a few specimens of Enteropneusta, the occurrence of which had been rendered almost certain by the presence in great abundance of Tornarias in the Madras Plankton. Among other types may be mentioned Amphioxus, Lingula, Edwardsia, Pennatulids, Sphenopus, etc. The Enteropneusta form the subject of the present paper.

I gladly take this opportunity of expressing my great indebtedness to Mr. Edgar Thurston, Superintendent of the Government Museum, Madras, who was so very kind as to place a small sum of money at my disposal for the purpose of dredging. I also wish to express in this connection my most grateful thanks to His Highness the Rajah of Cochin and to His Highness's late Prime Minister, Mr. P. Rajagopalachari, for their great generosity in enabling me to purchase much valuable zoological literature.

The Enteropneusta were dredged at depths of six to nine fathoms in mixed sand and mud. The specimens obtained were all imperfect. They belong to three different species belonging to the three families established by Spengel.

The Ptychoderidæ are represented by a single specimen, a

fragment $7\frac{1}{2}$ mm. long, and consisting of the proboscis, collar, and part of the branchial region. Unfortunately, the specimen was not of much use for anatomical purposes. Its external features (and what little it was possible to make out of its internal anatomy) agree so closely with Spengel's description of *Glossobalanus minutus* (*Ptychodera minuta*)—notably in the possession of the triangular "Kiemenfeld," which Spengel regards as characteristic of the species—that, notwithstanding the slight difference in colour, my specimen being more nearly white than the corresponding portion in Spengel's drawing, I have no hesitation at present in identifying it as a small specimen of that species.

A form identical with *Glandiceps haekii* represents the *Glandicipitidæ*. It is interesting to find this Japanese species here. A few specimens (all male and incomplete) of this were obtained; the largest of them measured about 45 mm. in length. The animal is drawn in fig. 1. When alive, the body of the animal was very contractile. I have very little to add to the descriptions of the animal given by Spengel and by its discoverer—Marion.

The proboscis is conical, and has a thick base and a pointed anterior end. Its dorsal surface is arched, and the ventral flat. Fig. 1 shows the proboscis in a fairly extended condition. A well-marked longitudinal groove is present on the dorsal side at the base, and a similar but less marked one on the ventral. The length of the proboscis when moderately extended is $6\frac{1}{2}$ mm., its basal breadth about 4 mm., and its basal thickness (dorso-ventral) a little over 3 mm. The collar is short, broad, and slightly depressed, its length, breadth, and thickness being $2\frac{1}{2}$ mm., $4\frac{1}{2}$ mm., and 4 mm. respectively. The anterior end of the collar is broader than the posterior. A little in front of the posterior end there is a ring furrow. The trunk immediately behind the collar is narrower than the collar, and compressed. Its breadth is, in this region, about $3\frac{1}{2}$ mm., and its thickness about 4 to $4\frac{1}{2}$ mm. It gradually becomes flatter and broader posteriorly, the posterior end of the largest fragment being $5\frac{1}{2}$ mm. broad.

The dorsal surface of the trunk is marked by two submedian ridges, which are correctly described by Spengel and Marion. In the posterior region of the trunk, at some distance behind the branchial region, two similar ridges (due to the thickening of the longitudinal muscles) make their appearance on the ventral side on either side of the median ventral groove. These ridges become narrower posteriorly. The lateral portions of the trunk—that is, the portions lying outside the submedian lines—are thicker in front than behind. The surface of the trunk is marked by transverse grooves and ridges both above and below. The colour of the animal agrees generally with that given by Spengel. The general colour is white or yellowish white on the ventral surface, which changes into yellowish brown on the dorsal, especially in the branchial region. Irregular dark brown patches are present on the dorsal surface of the proboscis and the collar. The ridges between the transverse grooves are marked by yellowish-brown pigment, especially on the dorsal side.

The internal organisation agrees very closely with Spengel's account. Spengel was able to see only the proximal portion of the vermiform process, having utilised the anterior portion of the proboscis for longitudinal sections. This, however, seems to be the only portion present. In one large specimen examined by me the process was only a little over $\frac{1}{10}$ mm. in length. The dorso-ventral septum of the proboscis stretches much farther forwards than the process. The vermiform process of this species is thus in a very reduced condition. As pointed out by Spengel, the chondroid tissue of the proboscis skeleton is very highly developed; the posterior limbs of the skeleton reach to the hind end of the collar. In the collar Spengel mentions a posterior epidermal invagination, and in his figure of a median longitudinal section he indicates a similar anterior invagination. This latter I have found in my sections, and one like it at the posterior end of the collar cord. They are both of them depressions into the actual nerve-tissue, and it is not clear to me why they are not called neuropores (the

rest of the axial canal of the collar-cord being broken up into the smaller spaces of the cord). They are certainly not like the anterior dermal pit which is present in the new species described here, and which has a proper epidermal wall. The arrangement of the intestinal pores is quite different in my largest specimen (the only one which possessed the post-branchial region) from that given by Spengel. Spengel mentions nine unpaired intestinal pores, the first being placed on the right side and the rest on the left, and, some distance behind these, three pairs of paired intestinal pores. In my series of transverse sections I counted about sixty of the former and six pairs of the latter. The arrangement of the unpaired pores is very irregular. They lie now on the left side, now on the right; some of them are paired, but the majority are unpaired. The gonads begin a little behind the anterior end of the branchial region, and extend into the commencement of the liver region. Marion's statement that they are confined to the branchial region is thus certainly not true of the males. The testes are paired, irregularly lobed, and transversely elongated bodies. These dorsally placed masses bend at the sides of the body, and extend into its ventral portion. They open by ducts along the submedian grooves.

Dolichoglossus bournei.—Two specimens of a new species of *Dolichoglossus* were obtained. The proboscis, collar, and a portion of the branchial region were alone present.

The animal is small. What at once enables one to assign it to its proper place is the great length of the proboscis. When moderately extended, it measured about 9 mm. in length, and after preservation about 6 mm. It is depressed, and its base is twice or three times as broad as the tip, its greatest breadth at the base being nearly 2 mm. The deep longitudinal groove present on the dorsal surface in the species *sulcatus* and *otagoensis* is absent. But in preserved specimens there is a shallow longitudinal depression on the dorsal side, extending forwards some distance from the base of the proboscis; there is a similar but less marked

one on the ventral side. As in other forms, these are, no doubt, caused by the contraction of the dorso-ventral septum of the proboscis. The anterior extension of the groove shows that the septum is not confined to the base of the proboscis. The proboscis is connected with the collar by a very thin neck. The collar measures nearly 1 mm. in length and nearly $1\frac{1}{2}$ mm. in breadth. Three annular grooves are present. The branchial region, which, like the collar, is nearly cylindrical, measures about $1\frac{1}{2}$ mm. from side to side. The larger of the specimens possessed about 18 mm. of this region, which was coiled ventrally, as shown in fig. 2. The sides of the trunk were transversely ridged, the ridges becoming more marked posteriorly.

The dorsal surface of the trunk is slightly flattened, and has a shallow, median, longitudinal groove containing the nerve-cord, and on either side of it a submedian groove containing the branchial pores and the openings of the gonads.

Both specimens were female, and were of a light brown colour. The tip of the proboscis and the collar were yellowish in colour.

I have not been able to make a complete study of the internal anatomy, but certain interesting points may be noted.

Proboscis.—The circular muscle is, as is usually the case in this genus, feebly developed. The longitudinal muscle forms a very thick layer, the fibres of which are not arranged in concentric rings. In this latter point, the present species agrees with *otagoensis*. The fibres have a remarkably straight course, as they are almost all represented by dots in transverse sections. The cavity of the proboscis is not merely confined to the base, but is present throughout the whole length of the proboscis. It is fairly wide—half as wide as the proboscis itself—in its anterior third, but between it and the base is reduced to a very narrow canal. At the base, the cavity is present as a very narrow space investing the basal organs in the usual way. The basal organs project a very short distance—about one tenth of its length—into the proboscis. The median mesen-

tery, however, extends farther forwards, and reaches up to the wider anterior portion of the proboscis cavity. The mesentery is more muscular in its posterior part than in its anterior, which is practically a band of connective tissue. It may be doubted whether this portion can be really called a mesentery, but there can be no doubt that the mesentery proper extends a considerable distance beyond the basal organs. This anterior extension of the mesentery is regarded—as far as I have been able to make out—as characteristic of the genera with a vermiform process, viz. *Glandiceps* and *Schizocardium*, and it is interesting to find it in *Dolichoglossus*, in which no vermiform process has been detected. The tip of the proboscis diverticulum is bent dorsally, as in *D. Kowalevski*. The diverticulum is hollow, but the cavity of the anterior portion is extremely narrow. In median longitudinal sections the neck of the diverticulum is seen to be very long, and to open into the buccal cavity far behind in the collar region. This posterior position of the opening (fig. 3) may be partly due to a slight retraction of the proboscis into the collar during preservation. The central blood-sinus is very conspicuous, and is distended dorsally just behind the heart vesicle. The heart vesicle is remarkably small. In a series of longitudinal sections each about $\frac{3}{400}$ mm. thick, the heart vesicle covers only ten sections. Its other dimensions can be gathered from fig. 3. Its posterior wall does not touch the wall of the proboscis. A similar reduction in the size of the heart is also mentioned in *Stereobalanus* (*Balanoglossus*) *Canadensis*. The body of the proboscis skeleton is long, and extends into the posterior region of the collar; the chondroid tissue is very poorly developed. Its posterior limbs reach to the hind end of the collar. The proboscis pore is placed on the left side of the median line at the posterior end of the neck of the proboscis.

Collar.—The collar has the usual structure. The dorsal mesentery is present throughout the whole extent of the collar, the ventral only in its posterior half. Transverse muscles are present in the ventral wall of the perihæmal

cavities. Peribranchial cavities are absent. The nerve-cord of the collar does not contain a central cavity, but numerous small spaces are present in it. The anterior end of the collar is sunk into a deep pit with folded walls and lying above the collar-cord. In transverse sections it appears as a crescentic space lying above, and extending laterally over the nerve-cord. The pit extends posteriorly more than half-way into the collar. The collar pores have the usual structure.

Trunk.—The body-wall is marked, as in other species of the genus, by the absence of a circular muscle. The longitudinal fibres form a thick band below the epidermis. Ventrally, on either side of the ventral mesentery, these fibres are scattered in the body-cavity, and a few are closely applied to the gut-wall, forming a feeble longitudinal musculature to it. Radial muscles are well developed between the outer walls of the branchial pouches and the body-wall; they are also scantily developed between the dorsal portion of the gut-wall and the body-wall. In the hypobranchial wall in the posterior part of the branchial region, outside the basement membrane of the alimentary epithelium, a thin circular muscular layer, consisting of extremely thin fibres, is visible. These fibres are also present in the epibranchial region. They have not been traced round the branchial pouches.

In the branchial system there is a histological detail which seems worth noting. A similar condition has been described only in one other Enteropneust, *Balanoglossus Kupferi*. The ciliated epithelium, instead of forming a single layer of low cells, consists of a layer of very thin columnar cells which have their numerous minute nuclei arranged in different levels. In stained preparations the epithelium shows a closely-packed mass of coloured dots, and gives a characteristic appearance to the branchial portion of the alimentary canal. As in other forms, this epithelium is restricted to the anterior and posterior faces of the branchial septa and tongues. The outer wall of the branchial tongue is not folded into the cavity of the tongue.

The ovaries reach quite to the anterior end of the branchial region. Median gonads are not present. The ovary (which is solid in the young stages) is a hollow sac: in specimens in which the ova are not fully developed, they are arranged round the lumen. Certain globular, fat-like bodies of varying sizes are also found among the ova. The ovary opens by the oviduct to the outside, externally to the branchial pores.

There can be no doubt that the form here described is different from the three species of the genus described by Spengel, and from the one described subsequently by Benham. I dedicate it to one to whom I owe much.

Of the two species of *Tornaria* found in the Plankton, one is *T. Krohnii* and is very common. This has been previously recorded from the Mediterranean and from the European and American Coasts of the Atlantic. *Glossobalanus minutus*, which occurs here, has also been recorded from the Mediterranean and from the American Coast of the Atlantic. This may be a mere coincidence, of course; but it may also be that *T. Krohnii* is the larva of *Glossobalanus minutus*.

The other species of *Tornaria* cannot be identified with any of those described by Spengel. Figs. 5 and 6 represent the larva from the ventral and dorsal aspects. It is about $1\frac{1}{2}$ mm. long. With the help of Spengel's terminology, this form may be characterised as follows:—The ventral lobes of the oral area are shallow and broad, and are secondarily lobed. The portion of the pre-oral area which lies below these ventral lobes and to the sides of the mouth is also encroached upon on its outer side by secondary lobes of the oral area. The upper dorsal lobes have secondary and tertiary lobes. Lower dorsal lobes are well developed. There are no lateral lobes. The ventral saddle of the postoral area is long and narrow, as in *T. agassizi*. There is no secondary perianal ring of cilia. Round patches of yellowish-brown pigment are found along the course of the ciliated bands. They are placed on the side of these bands, turned away from the oral area. They are also found along

the perianal band of cilia, on the side turned towards the mouth. A smaller ring of such patches, often appearing as slight elevations, is present round the anus. These, no doubt, represent a vestigial secondary perianal ring. These patches agree in colour with the transversely elongated patches found on the body of *Glandiceps haekii*, and possibly the larva belongs to this species.

It may be added here that, in his monograph, Spengel mentions two forms, *Ptychodera* (*Chlamydothorax*) *Ceylonica*, and *Tornaria grenacheri*, which were obtained in Ceylon.

MADRAS;

October 2nd, 1902.

EXPLANATION OF PLATE 10,

Illustrating Mr. K. Ramunni Menon's paper on "Enteropneusta from Madras."

FIG. 1.—Dorsal view of *Glandiceps haekii*. $\times 3$. The gonads were sketched from preparations cleared in clove oil.

FIG. 2.—*Dolichoglossus bournei*. $\times 6$. The gonads were sketched from clove-oil preparations. Dorsal view.

FIG. 3.—Median longitudinal section of Fig. 2. *con.tis.* Connective tissue. *pr.cæ.* Proboscis cælom. *d.v.s.* Dorso-ventral septum. *N.B.* The dorso-ventral muscle-fibres ought not to have been drawn in the anterior portion. *gl.* Glomerulus. *bl.sin.* Blood-sinus. *v.div.* Ventral diverticulum of the proboscidial diverticulum. *ep.div.* Anterior epidermal pit. *c.c.* Collar-cord. *sk.* Body of the proboscis skeleton. *p.h.* Perihæmal cavity. *h.* Heart vesicle.

FIG. 4.—Transverse section of the branchial region of Fig. 2. *d.n.c.* Dorsal nerve-cord. *v.n.c.* Ventral nerve-cord. *g.p.* Genital pore. *r.m.* Radial muscle-fibres. *br.s.* Branchial septum. *br.t.* Branchial tongue. *ov.* Ovary. *c.m.* Circular muscle-fibres of gut wall. *l.m.* Longitudinal muscle.

FIG. 5.—New species of *Tornaria*. Seen from the ventral aspect. $\times 40$. The oral area is shaded.

FIG. 6.—New *Tornaria*, from the dorsal side. Oral area shaded.

On *Planktonetta atlantica*, Borgert.

By

G. Herbert Fowler, B.A., Ph.D., F.Z.S.

With Plates 11 and 12.

It is now many years ago that Richard Hertwig¹ founded the group of Tripylarian Radiolarians. Since that date Haeckel² has added enormously to the list of known forms in his monumental monograph; yet but little attention has been paid to the intimate structure of these curious organisms. As there were several comparatively unbroken and numerous broken specimens of an unusual Phæodarian type among the Plankton which I collected in the Bay of Biscay on H.M.S. Research, in 1900, it seemed worth while to study them somewhat more systematically than has usually been the lot of members of this group.

Dr. Borgert founded the species under the name of *Gazelletta atlantica*³ in 1901, giving a short preliminary diagnosis and two cuts. Later on, he recognised the generic differences between *Gazelletta* and the present form, and established for it the name *Planktonetta atlantica*.⁴ His material, however, was evidently considerably broken,

¹ R. Hertwig, 'Der Organismus der Radiolarien,' Jena, 1879, 4to.

² E. Haeckel, 'Chall. Rep., Zool.,' "The Radiolaria."

³ 'Nordisches Plankton. xv: Nordischen Tripyleen-Arten,' von Dr. A. Borgert, p. 39.

⁴ Borgert, "Mittheilungen über die Tripyleen-Ausbeute der Plankton Expedition," 'Zool. Jahrbüchen' (Abth. Syst.), xvi, 571.

and in particular did not show the characteristic structure which, for want of a better word, I have termed the "float." He was therefore kind enough to give me permission to describe the animal in detail, a permission for which I beg here to express my thanks. In the hurry of work at sea these small and transparent organisms escaped notice; they were neither examined alive nor specially prepared for histology. I can, therefore, only hope that the present bald and incomplete description may be supplemented by some one with leisure and opportunity to study the living material, notably as regards that bewildering complex, the phæodium.

For purposes of description the organism may be divided into the shell, with shell-mouth and arms, the float, the central capsule and intra-capsular contents, and the phæodial or extra-capsular region.

The aboral region of the SHELL (figs. 1—3) would be nearly spherical but for a protrusion in the anterior direction. It is homogeneous, and bears minute (and, I think, solid) echinulations. It stains deeply in hæmatoxylin, and appears to be of the same character as the rest of the skeleton, but softer and less resistant to the action of strong alkalies and acids; in raising to alcohols and paraffin it crumples considerably. It is transparent and slightly refractile, and I have only been able to detect one layer in the aboral region; as it nears the mouth, however, it splits into two layers (figs. 4, 8, 9). The shell-mouth is divisible into three zones; the most aboral of these clearly shows two layers, the inner of which is invaginated to form pits, which give it, from outside, a honeycombed appearance. The next zone above this appears externally to be homogeneous, and is perforated by a ring of fine pores, oval or circular, of unequal sizes. The zone of the lip, like the lowest zone, presents a honeycombed appearance, due, in this case, to laminae between the two layers which divide the contained space into irregular polygons, generally hexagons. The actual lip is highest anteriorly, lowest posteriorly (fig. 5); the actual opening is circular (fig. 6). The shell-mouth as a whole is convex or ogival in section,

the pores being placed at about the most prominent part of the curve.

From the edge of the lip spring the arms. These are eight in number ; six of them are arranged as a right, a left, and an anterior pair, all of which radiate from the lip nearly at right angles to the longitudinal axis ; there is also an upright pair, taking origin right and left of the anterior pair, which lie at first nearly parallel to the long axis. The general direction of the arms varies in different specimens, apparently according to the amount of bad usage received in the tow-net ; but the right and left pairs mostly bend aborally and posteriorly, the anterior pair aborally and outward, the upright pair anteriorly. The arms vary considerably in length, the right and left pairs being the longest, the upright and anterior pairs generally subequal. They are tubular, the cavity being subdivided by laminae (fig. 7), and exhibit, except at the tip, two layers,—an outer, less refractile, which is continuous with the spines, and an inner, more refractile layer, of which the laminae form a part. The distribution of the spines is very irregular, but near the phæodium they seem to be in pairs, more or less opposite to one another, each pair in a plane at right angles to its immediate neighbours. Distally the arrangement is more irregular, and the spines closer together. Dr. Borgert's specimens appear to have been somewhat more variable than mine ; I therefore translate his description.¹ " At the distal end the arms run out into two to four diverging branches. These terminal branches are simple or forked, in other cases with three, four, or even more tines ; in this respect not only do the arms of the same specimen often show variations, but even the terminal branches of one and the same arm may be dissimilarly constructed. The surface of the arms is beset with racemose lateral spines ; these carry on their numerous long thread-like branches a terminal circlet of four, more rarely five, short, thick, backwardly directed hooks ; a little beyond these the thread carries another whorl of three to five (generally four) somewhat larger and thinner

¹ ' Nordisches Plankton,' op. cit. supra.

hooks." My specimens showed never less than three or more than four terminal branches. The branching of the lateral spines seemed always to be regularly dichotomous, and to end in from eight to thirty-two fine "tuning-forks" (Dr. Borgert's threads). Of the two whorls of hooks which he figures I have once or twice caught a glimpse in making preparations, but they have almost invariably been broken away in my specimens.

The internal spines of the region of the shell-mouth are somewhat complex. In the anterior portion of the mouth, all the way round, a ring of spines (sp. i) radiates inwards below the edge of the lip across the circular opening of the shell; these branch to form a fine meshwork supporting the extra-capsular protoplasm and phaeodium. The posterior portion of this ring passes over the lip to the outer edge, and is directed outwards, the spines here being shorter and more numerous (sp. ii); these also branch to form a meshwork which lies on the float, and, as far as I can ascertain, becomes actually continuous with it, fastening float to shell. A few spines, given off from the body of the shell itself (sp. iii) and from the bases of the most posterior arms right and left, are similarly inserted on, and help to attach, the float. Spines from the float itself also ramify into the extra-capsular region (sp. iv). A meshwork of very fine character takes origin also from the lowest or pitted zone of the shell-mouth, and ramifies in and on the diaphragm; a specially strong bundle of fine spines belonging to this system, left after treatment with strong warm acids, is generally to be found on the inner anterior aspect of the mouth (sp. v). Presumably all the meshworks of the phaeodial region are continuous with one another; but as they disappear entirely in cleaning the skeleton of phaeodium by any method that I have tried, they can only be made out by sections and teased preparations; the sections, at any rate, appear to point to continuity throughout.

The FLOAT is nearly spherical, but somewhat flattened or dented on the side which faces the phaeodial region; it is

hard, brilliantly refractile, and transparent, and is dissolved by treatment with warm strong acids. It exhibits over the greater part of its circumference two layers, both of which are homogeneous and smooth; the inner softer, and generally shrunk in preparation for sections; the outer harder, splintering before the razor, and retaining its spherical shape. The inner layer stains deeply with hæmatoxylin; the outer does not stain at all, except centrally where it faces the phæodial region; in this part both layers look alike in sections, and are either intimately connected or fuse in places. What sometimes in sections resembles a third layer is probably due merely to the coagulation of the fluid contents of the float.

If I am right in thinking that the meshwork and lip spines are actually continuous with the float, then the float is merely a part of the general skeleton, and presumably has been evolved from a skeletal meshwork between arms such as occurs in many Phæodaria (e. g. the allied *Gazellella*), and may prove perhaps to represent one or more pairs of arms, arched over and fused at their ends, such as Borgert¹ has described in species of the allied *Medusella*. When the float has been broken away its loss could not be suspected, as its connection with the shell is only through very fine spines and meshwork.

Across the narrowed neck of the shell (figs. 8, 9) stretches a circular diaphragm of fibrous character; its edge is thickened, and the upper part of the thickening is inserted by processes into the pits of the lowest zone of the shell-mouth below the pores. Below this lie the intra-capsular protoplasm and nucleus, enclosed below (aborally) by a lining membrane, conspicuous in fig. 1; the latter becomes greatly folded and shrunk in preparation for sections (fig. 8), hence my interpretation of the structures present in this region is merely provisional, in default of fresh or specially preserved material.

We may presume that there exists something internal to the shell corresponding to the characteristic CENTRAL CAPSULE

¹ 'Nord. Tripyleen-Arten,' pp. 35, 36, figs. 42, 43.

of Radiolaria. In the lining membrane I can only identify one layer with certainty, and there is therefore a presumption that this is the homologue of part of the central capsule; but it is softer and less refringent, and it stains more deeply than is usually the case. This lining membrane is clearly traceable as a thick and deeply stained line as far as the upper angle of the mass of "intra-capsular" circumnuclear protoplasm; but immediately below the diaphragm it is less stained, thinner, and more refractile. I incline to regard the diaphragm as a complementary thickening of the central capsule; in my sections the capsule and diaphragm are never continuous, yet appear to have been so in life, for while the upper angle of the thickened edge of the diaphragm is always tucked neatly into pits of the skeleton (as already mentioned), the lower angle, of varying length and ragged appearance, hangs down into the shrinkage space between capsule and shell (*d. i.*, fig. 8); it has every appearance of having been attached to something, probably to the capsule. While, therefore, fig. 8 represents the actual topographical relations seen in longitudinal section, they have been restored in fig. 9 to what I believe to have been their true positions and connections.

The INTRA-CAPSULAR PROTOPLASM, as is apparent from the various figures, lies immediately below the diaphragm, and has a central aboral swelling due to the nucleus. It is coarsely granular, and above (orally) but not below the nucleus is more or less vacuolated. Laterally it is highly vacuolated, the strands passing outwards to the lining membrane, but there is no trace of such strands having been given off below the nucleus. On its upper or diaphragmatic face it projects in the manner shown in figs. 8, 9, and 10; the projections are laminated, and appear to have been inserted into the diaphragm, serving to hold the central mass of protoplasm in place; they penetrate through the thin refractile central capsule (fig. 10); at their bases the protoplasm is closer in texture and more finely granular than elsewhere. I

have seen no trace of oil globules or of the other inclusions so common in some Radiolaria.

At the upper outer angle of the protoplasmic mass, and at the most anterior point of its circumference (fig. 9), the protoplasm is close and finely granular; from this point a bundle of fine tubes, about seventeen to twenty-five in number, penetrates through the central capsule and diaphragm, and leads upwards towards a mass of extra-capsular protoplasm, which is free of phæodial corpuscles. This bundle of tubes corresponds to pore-areæ, astropyles, etc., in that it connects intra-capsular and extra-capsular protoplasm. It is at first difficult to detect, the whole bundle being only about 11 to 25 μ across, an individual tube less than 1 μ , but I have found it in every series of sections. On the other hand, I have failed to find any further opening in the central capsule, and do not believe that such exist; Planktonetta, therefore, would seem to be Phæodarian (Haeckel), but not Tripyllarian (Hertwig). The structure of the nucleus cannot be accurately determined from specimens indifferently preserved in formalin. It appears to be bounded by a definite membrane, and to exhibit numerous large round chromatin granules, with patches of a more lightly stained plasma. All the nuclei cut were in one phase, apparently a resting phase.

With regard to the EXTRA-CAPSULAR PROTOPLASM, a large irregular mass lies somewhat anteriorly near the ends of the communicating tubes (fig. 9). Elsewhere it is so closely packed with phæodial corpuscles and other inclusions as to be hardly visible in sections. The majority of the phæodial corpuscles, as seen in a teased preparation in glycerine, can be divided into the brown and the clear corpuscles. These brown corpuscles are fully charged with coarse and fine granules, crystals (?), etc., to which they owe their colour. It would seem that some of these corpuscles are excretory, almost "phagocytic;" fig. 12, *a*, shows one of them containing an organism which, whether food or parasite, appears to be a young specimen of the organism drawn in fig. 15 to the same scale. A similar brown corpuscle in fig. 12, *c*, contains a

pyramidal plate of what looks like chitin; fig. 12, *e*, shows the inclusion of flat ragged plates of the same substance, and I have twice noticed a portion of a Radiolarian or Diatomaceous skeleton similarly included. Inclusions and coloured granules alike point to the excretory nature of these brown corpuscles. They may fairly be compared with the amœboid fragments of the excretory splanchnic epithelium found in the cœlom of many Chaetopoda.

The clear corpuscles are probably of more than one kind. They often have such a fibrous appearance internally as is presented by an irregularly wound ball of fine cotton. In some specimens clear corpuscles without this fibrous look appear to be undergoing an irregular segmentation (fig. 13), the larger ones then appearing to lie inside a fine membrane. In one specimen, stained and teased in oil of cloves, almost every corpuscle in the phæodium was more or less morulated (fig. 14). In the morulæ the ends of the spheres are apparently connected with a central mass (fig. 14, *e*); their outer ends generally are more deeply stained than the inner. It is possible that this stain is due to something in the nature of a nucleus. I can make no suggestion as to the nature of these segmented bodies, which are not plentiful in every specimen. Other inclusions noticed in the phæodium were (*a*) commonly, spherical, homogeneous, highly refractile, and colourless bodies; (*b*) rarely, deep brown concentrically laminated irregular spheres; (*c*) commonly, plates of what looked like chitin, generally more or less completely folded; (*d*) once, a minute crustacean mouth-part; (*e*) very rarely, a fragment of Diatomaceous or Radiolarian skeleton; (*f*) once, what looked like the primary chamber of a Globigerina; (*g*) twice, the organism figured in 12 *a* and 15. On the whole the indications of food are curiously infrequent, those of excretion prominent.

A few words on methods may not be out of place. The phæodium is so opaque that solid preparations are not satisfactory, but Grenacher's alum carmine yields fair results after days of immersion in acid alcohol. Borax carmine is unsatis-

factory from every point of view. For sections, Delafield's hæmatoxylin for three to six hours yields excellent results alike for skeleton, phæodial corpuscles, and protoplasm. As regards the skeleton, I failed to find anything which would remove the phæodial corpuscles without also removing the finer spines and meshwork, after trying various combinations of organic and inorganic acids, alkalies, and pepto-hydrochloric digestion. Haeckel's prescription, pure sulphuric acid with a drop of fuming nitric at 60° C. for an hour or two, yields beautifully clean preparations of the stronger parts of the skeleton; but the float, the lower part of the shell, the finer spines, and the entire meshwork disappear under its action.

SUMMARY.

Planktonetta is a Phæodarian Radiolarian possessing in addition to the ordinary shell of the Medusettidæ a hollow skeletal sphere, larger than the shell, here termed a float. The body of the shell is of softer nature than its mouth. The mouth of the shell carries eight spined arms, and gives origin inwards to a skeletal meshwork across the aperture, which serves to connect float and shell, and to support the phæodial complex. Between the mouth of the shell containing the extra-capsular protoplasm, and the body of the shell containing the intra-capsular protoplasm, lies a fibrous diaphragm, which may be regarded as a part of the capsule. The central capsule lines the body of the shell; it contains the nucleus and vacuolated protoplasm, the latter attached by special processes, which perforate the capsule, to the diaphragm. A bundle of fine tubes leads from the intra-capsular to the extra-capsular protoplasm, perforating capsule and diaphragm. The extra-capsular protoplasm, permeated by the skeletal meshwork, contains the phæodial corpuscles of various kinds in vacuoles. Of the structures here described the float, the diaphragm, and the single bundle of tubes of communication are unparalleled among Radiolaria.

EXPLANATION OF PLATES 11 AND 12,

Illustrating Dr. G. H. Fowler's paper on "*Planktonetta atlantica*, Borgert."

All the figures have been drawn with the Abbé camera.

In Figs. 1—3 the spines of the arms have been omitted.

FIG. 1.—View approximately from the right side and somewhat anteriorly, the left pair of arms omitted. Below is the shell, containing the central capsule; into the latter projects the dark intra-capsular protoplasm, slightly trefoil-shaped, with two fainter wings, probably produced by the vacuolated protoplasm (cf. Fig. 9). The shell is narrowest just above this region, and expands at the mouth, which is largely covered by the dark granular phæodial or extra-capsular protoplasm and corpuscles. The float lies posteriorly. $\times 6\cdot6$.

FIG. 2.—From the oral aspect, looking down on the phæodium; behind this the outline of the shell body. The float is clearly seen to lie posteriorly. $\times 6\cdot6$.

FIG. 3.—View aborally and slightly anteriorly, the anterior prominence of the shell body towards the observer. $\times 6\cdot6$.

FIG. 4.—Small portion of the mouth of the shell from the outside, showing the zone of polygons at the lip, the middle smooth zone with pores, the lower pitted zone passing into the homogeneous shell, two of the spines of which are also represented. $\times 140$.

FIG. 5.—Mouth of the shell viewed from the posterior aspect, showing the origin of the arms, all spines and the polygonoid structure omitted. $\times 32$.

FIG. 6.—Mouth of the shell from above (orally) looking down into the circular aperture, only some of the long spines (sp. i) remaining. $\times 48$.

FIG. 7.—*a*. Low-power view of about two thirds of an arm, the spines broken. $\times 36$. *b*. Termination of an arm, showing the two layers of which it is composed, and the laminae which cross its lumen. One lateral spine showing dichotomous branching into sixteen has been drawn; for the terminal whorls of hooks the reader is referred to Dr. Borgert's paper. Of the three terminal branches of the arm only one has been drawn, with three tines; the cavity of the end branches is not continuous with the general lumen of the tube. $\times 140$.

FIG. 8.—Part of an antero-posterior section to show the topographical relations of the diaphragm (*d.*), its free edge (*d. i*), the thicker lower (*c. c. i*) and thinner upper (*c. c. ii*) parts of the central capsule, as actually presented in sections. $\times 90$.

FIG. 9.—Semi-diagrammatic antero-posterior section of the body of *Planktonetta atlantica*, based on a camera lucida drawing, the central capsule restored to its supposed connections. The intra-capsular protoplasm, compact below, slightly vacuolated above, is greatly vacuolated laterally, the meshes running out to the central capsule; this lateral protoplasm is apparent also in Fig. 1. Orally the thin central capsule is perforated by the processes for attachment to the diaphragm. The diaphragm, which stretches right across the shell, is thickened at its edge so as to present a triangular section; it is inserted above into pits of the shell, and below has been drawn as if either continuous with or inserted into the central capsule. Near its anterior border the diaphragm is perforated by a bundle of tubes; by these the intra-capsular protoplasm communicates with the anterior mass of extra-capsular protoplasm which is free from phæodial corpuscles. Through this mass and through the whole phæodial complex runs the skeletal meshwork produced by the branching of the various spines. Only portions of this have been drawn; it supports the protoplasm, and the phæodial corpuscles lie in vacuoles in its meshes. \times circa 120.

FIG. 10.—A process for attachment of the intra-capsular protoplasm to the diaphragm, perforating the central capsule. \times 520.

FIG. 11.—Portion of the skeletal meshwork of the phæodium, produced by the branching of three stouter spines. Slight webs occurring at the more important nodes have been omitted from the drawing. \times 280.

FIG. 12.—Brown corpuscles of the phæodium, with various inclusions (p. 139). \times 520.

FIG. 13.—Segmenting varieties of the clear corpuscles of the phæodium (p. 140). \times 520.

FIG. 14.—Segmented corpuscles of the phæodium from a specimen in which the majority of corpuscles ranged between stages represented in *c* and *d*. In *c* are represented three isolated segments from such a morula as *d*, showing their attachment centrally and the darker stained area peripherally. \times 520.

FIG. 15.—Organism from the phæodium. \times 520.

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CONTENTS OF No. 186.—New Series.

MEMOIRS:

	PAGE
On <i>Peripatus guianensis</i> (sp. nov.). By RICHARD EVANS, M.A., D.Sc.(Oxon.), Curator of the Museum, Georgetown, British Guiana. (With Plates 13 and 14)	145
Observations on Ovarian Ova and Follicles in Certain Teleostean and Elasmobranch Fishes. By WILLIAM WALLACE, B.Sc. (With Plates 15 to 17)	161
A New <i>Koenenia</i> from Texas. By AUGUSTA RUCKER, of the Uni- versity of Texas, U.S.A. (With Plate 18)	215
<i>Oligotrema psammites</i> : a New Ascidian belonging to the Family <i>Molgulidæ</i> . By GILBERT C. BOURNE, D.Sc., F.L.S., Fellow and Tutor of New College, Oxford; University Lecturer in Comparative Anatomy. (With Plates 19 to 23)	233

On *Peripatus guianensis* (sp. nov.).

By

Richard Evans, M.A., D.Sc.(Oxon.),

Curator of the Museum, Georgetown, British Guiana.

With Plates 13 and 14.

CONTENTS.

	PAGE
Introduction	145
External Characters	149
Internal Characters	153
Male Generative System	153
Female Generative System	154
Summary of Characters	154
Concluding Remarks	155
Explanation of Plates	159

INTRODUCTION.

To add another species to the already somewhat large number of the New World members of the family Peripatidæ will probably seem to many zoologists to be unwarranted presumption, for within the last few years the number of species from this part of the world has been more than doubled—a result, to some extent, of redescribing old material rather than of discovering new forms. However, the species under consideration in the present paper cannot be identified with any of the already known ones; and whatever view we choose to adopt regarding the validity of some of the species which have been made, I am of opinion that no one will doubt,

after perusal of the facts which will be recorded in the coming pages, that *Peripatus guianensis* is a new species.

Perhaps, before proceeding to the actual description, it would not be out of place to refer to the utter uselessness of much that has been written on the Peripatidæ, especially as regards the colour and dimensions of preserved specimens. In the first place, observations made on the colour of specimens preserved in either alcohol or formalin have little or no value. The colouring matter existing in the skin of the neotropical Peripatidæ is gradually abstracted by the above-mentioned reagents, and the characteristic markings and patterns, when such exist, disappear in a few days. Ultimately the animal becomes quite colourless, the colouring matter being dissolved in the preserving liquid, and giving it a more or less brownish tint. Unfortunately this is only too true of *P. guianensis*, which is the subject of the present paper. After the specimens had been in either spirit or formalin for a few days the characteristic markings had disappeared so completely that no one would have suspected the presence of two distinct species among the specimens in my possession, unless he took into consideration some character other than the coloration, although in the living animal the distinctive markings of *P. guianensis* were so evident that the black man who collected the specimens for me was able at a glance to separate the individuals belonging to this species from those of the other species found in Demerara. In consequence, I have been forced to the conclusion that observations made on the coloration of neotropical forms of the Peripatidæ, to be of any value, must be made on the living animal.

In the second place it is fashionable, in describing a new species or in redescribing an old one, to give the exact dimensions of the specimens. The length, depth, and width of the animal are carefully recorded, and very often tabulated; the length of the antennæ and the distance between the successive pairs of legs are observed with great care, but all to no purpose, save to show that the author is capable of paying

minute attention to details, however small and insignificant they may be. Such measurements are not only useless, but they are positively harmful, for they are unconsciously being used as characters having considerable specific value, although it is absolutely clear that from the point of view in question they are of no importance. To arrive at this conclusion there is no need but to consider the fact that in any collection consisting of a fair number of individuals of a particular species there are specimens the dimensions of which are at least three times that of the smallest ones, although the latter are as perfect as the former from the structural point of view. The dimensions of any individual specimen depend on the age of the animal at the time it was killed, and consequently have no specific value. Again, the dimensions of a dead *Peripatus*, to a great extent, depend on the method adopted to kill the animal. Owing to the presence of circular, longitudinal, and oblique muscles in the body-wall, a *Peripatus* measuring, when alive, about 80 mm. in length, is capable, at death, of contracting itself to about 50, or even 40 mm. The amount of contraction taking place varies with the reagent used, as well as with the degree of concentration of that reagent. Consequently the dimensions of a dead *Peripatus*, when given in a paper, do not increase the value of the account, for they have no constant relation to the size of the living animal, the length, depth, and width of which vary according to the age of the individual under consideration.

In the third place, whether the legs are long and slender or short and stumpy, and whether the successive pairs are situated at a distance from or close to each other, are points of no importance in a dead specimen; nevertheless they are carefully observed and recorded. If the specimen dies fully extended the chances are that the legs are also fully extended, and, in consequence, are long and slender, and placed at a distance from one another; but if the specimen dies in a contracted condition the chances are equally in favour of the legs being contracted, and, in consequence, of

their being short and stumpy, and placed close to one another. Hence the facts recorded as to the shape and relative position of the legs in a dead *Peripatus* have no practical value. Because the usually recorded facts as to the coloration and the dimensions of preserved specimens have no value, in the present paper the reader will look in vain for the facts in question.

The material to be described in the coming pages was collected for me by a black man aback of a plantation situated on the east bank of the river Demerara. The specimens were collected during the first half of August, 1902, and consisted in all of nine individuals, which were distributed between the sexes in the ratio of eight females to one male. This fact is in accordance with the almost invariable rule that in any collection of *Peripatus* the females are more numerous than the males.

In looking at this small collection of nine animals the idea that occurred to me at first was that I had been so fortunate as to come across the male of *Peripatus im-Thurmi*, which has, up to the present, remained undiscovered; but on dissecting one of the specimens I found that the animal being examined was a female, and I was forced to the conclusion that I must have discovered a new species. The specimens were found on more or less swampy ground, under the remains of rotten leaves and dead tree trunks. Some of them were kept alive at the museum in a glass-covered box, in which was placed a quantity of the soil, leaves, and rotten wood which they usually inhabit. To all this was added enough water to make the contents of the box as damp as the man who collected the specimens thought their customary habitat was, and the result seemed to be a veritable swamp. Specimens belonging to another species collected in the same locality and under similar circumstances still thrive well in the artificial swamp described above.

EXTERNAL CHARACTERS.

The Dimensions of the Living Animal.—The greatest length the male specimen seemed to be capable of, even when in motion, was about 35 mm. The female specimens seem to consist of individuals of all ages, ranging from a young one containing no embryos, and measuring about 30 mm. in length when in motion, to older ones full of young in different stages of development, and measuring, when fully extended, no less than 80 mm. in length. In proportion to their length they seem to be stouter than *P. im-Thurmi*. Their girth, however, depends to a considerable extent on the state of development attained by the young which they contain. In the moving animal the legs are slender, and situated at a considerable distance from one another, but on contraction of the animal, either when irritated or at death, both the body and the appendages shorten and become thicker, and the spaces between the successive pairs of legs almost disappear in spite of the fact that in the living animal the width of the spaces in question is to that of the leg as seven is to five. This latter fact demonstrates in the most clear way the utter futility of giving the dimensions of dead specimens, which are invariably more or less contracted.

The Colour of the Living Animal.—The colour varies considerably in tint; nevertheless the pattern is maintained. On the dorsal aspect the colour is some shade or other of brown, and on the ventral of grey. The variation occurring in different individuals is brought about by the presence or absence of a pinkish constituent, which gives the animals' colour a warmer or colder tone. The mid-dorsal position is occupied by a chocolate-coloured line of a decidedly dark tint, with lozenge-shaped areas roughly corresponding to the appendages arranged on it. Smaller areas of a similar shape may be intercalated so as, to some extent, to interfere with the apparently segmental arrangement of the bigger ones. On either side of the line in question is found a zigzag one

much lighter in tint and warmer in tone than either the median line and its lozenge-shaped areas or the flanks of the animal. The sides of the animal agree in tint with the median dorsal line, but become somewhat lighter in the immediate neighbourhood of the walking appendages. The ventral surface is grey in colour, but with a pinkish constituent in some individuals. The spots corresponding to the ventral organs, and situated mid-ventrally between the appendages, are always a lighter grey. In the majority of cases the antennæ are somewhat darker than the dorsal surface. The darker and lighter areas on the dorsal aspect are produced by a corresponding difference in the colour of the papillæ, which are dark brown in one case and light brown in the other.

The Skin, with its Ridges and Papillæ.—The skin is thrown into folds or ridges, on which the papillæ, both primary and accessory, are situated. In the mid-region of the body there are about twelve folds to every pair of appendages. As a rule, seven of these pass uninterruptedly from the mid-dorsal line over the sides and between the appendages to the ventral surface. Of the remaining folds, at least two terminate about halfway between the mid-dorsal line and the legs, while the other three reach the appendages and there end. The continuity of the folds is broken at the mid-dorsal position by a very narrow and clear line, which is visible only with the microscope. On either side of the line in question, in the spaces between the folds, the openings of the tracheæ are situated.

On the dorsal aspect of the head the papillæ present a diffused arrangement. Around the base of each antenna they are arranged in three or four more or less complete rings, on one of which the eye is situated. The rings in question pass between the antennæ, and those on either side are not separated by a row of papillæ passing from the area on top of the head, on which the papillæ are irregularly arranged, to a similar area situated on the ventral surface in front of the mouth.

On the folds of the skin two kinds of papillæ are found: first, the primary papillæ, large in size, and differentiated to apical and basal portions; and secondly, the accessory papillæ, smaller in size and undifferentiated. As a rule, the basal portion of the primary papillæ slopes very gradually, and has an extensive outline which stretches across the entire fold (Pl. 14, figs. 1 and 2). The basal outline of the primary papillæ is far more distinct near the mid-dorsal line than it is lower down on the sides where the bases of the papillæ run into one another. On the limbs the basal portion may assume an almost cylindrical form. The apical portion when fully extended is almost invariably cylindrical in shape, and carries a spine on its top. The basal portion is covered by short broad scales, but the apical one by long narrow ones. The accessory papillæ present a considerable amount of variation, according to the position which they occupy. Near the mid-dorsal line they stretch across the entire fold, and, as a rule, only one is found between the primary papillæ (Pl. 14, fig. 1); but near the appendages they are small, and do not cover the fold from side to side, for several of them occupy the space between the primary papillæ (Pl. 14, fig. 2). It seems that the accessory papillæ situated on the sides have been produced by the breaking up of larger ones, similar to those found in the vicinity of the mid-dorsal line.

The Mouth.—The mouth has the usual shape and position, and is surrounded by large papillæ which are yellowish white in colour. Half a dozen of these papillæ form a horseshoe, situated in front of the mouth, the remainder being disposed in a ring outside. When the mouth is in a contracted condition the complete ring seems to be inside, and the horseshoe outside. The appearance the papillæ surrounding the mouth present depends on the degree of contraction.

The Genital Aperture.—This opening is situated between the penultimate pair of appendages, and is surrounded by papillæ which are slightly enlarged. In some of the specimens the area round the genital aperture is raised, so

that the actual opening is placed on top of a conical elevation.

The Antennæ.—Immediately behind the antennæ the papillæ on the head are arranged in three or four more or less complete rings, on the second of which, counting from in front, the eye is situated. The base of the antenna, consisting of two segments carrying the usual papillæ, is followed by a third segment, on which the scales are arranged in quite a simple and unmodified way. The segment in question is followed by forty-two others similar in character to the first two. Thus the whole antenna consists of at least forty-five segments.

The Jaws.—The two blades of the jaws present the same structure as they do in most neotropical species. The outer blade has one big tooth, on the inner side of which is situated a small denticle. The inner blade has a large tooth, on the inner side of which is a small denticle followed by a diastema, in which a vestige of a second denticle may be seen. A row of ten or eleven small denticles occurs on the inner side of the diastema.

The Oral Papillæ.—These organs have the same structure as in other South American forms, and call for no further remarks.

The Walking Appendages.—The number of walking appendages present vary from twenty-four to twenty-eight pairs. The single male specimen in my possession has only twenty-four pairs, one of the females has twenty-seven pairs, the remaining seven specimens being possessed of twenty-eight. The appendages carry four spinous pads, and on those situated in the mid-region of the body there may be a small remnant of a fifth. Each leg of the last pair has only two pads, which are somewhat reduced in size. Of the legs of the penultimate pair each one carries three pads. The coxal organs are well developed, but in the majority of cases they are retracted so as to present the appearance of grooves. The renal apertures are situated on the inner side of the coxal organs, with the exception of those of the fourth

and fifth pairs of legs, on which they are placed between the third and fourth spinous pads on the top of a papilla (Pl. 14, fig. 5). In the male, sexual papillæ are found on the antepenultimate pair of legs (Pl. 14, fig. 6).

The feet present the same general appearance as in the majority of American species. There are two primary papillæ in front of the distal end of the foot and one behind. On the ventral aspect of the foot there are two pairs of elevations, on every one of which there are three spines, twelve in all, which is the maximum, but not the minimum number of spines observed on any foot. In the cases in which there were fewer spines than twelve some of them had probably been lost.

The number of appendages present in several embryos, in which all the legs had already appeared, have been counted, and have been found to vary from twenty-four to twenty-eight pairs, numbers which represent the extremes found in the adults. It seems highly probable that specimens with fewer than twenty-four or with more than twenty-eight pairs will prove to be rare exceptions in *Peripatus guianensis*.

INTERNAL CHARACTERS.

As far as I have been able to make out from dissection, the internal anatomy agrees with that of the most typical of the neotropical species, and there is no need but to point out that certain organs of importance do exist. The alimentary tract is quite normal, and is surrounded by the numerous branches of the slime glands, which extend almost to the posterior end of the animal. The organs which demand special notice are those which constitute the male and female generative systems.

The Male Generative System.—The male generative organs are quite typical of those of the South American *Peripatidæ* (Pl. 14, fig. 9). The testes are tubular in form, and are freely suspended in the body-cavity. Each testis

communicates with a seminal vesicle which is oval in shape, and debouches into a vas deferens (Pl. 14, fig. 9, *v. d.*). The right vas deferens passes backwards and, after a short course, crosses to the left side, passing under the ductus ejaculatorius in doing so. Having crossed over it unites with its fellow to form the common duct, which is coiled on the left side of the intestinal tract, and which ends in the ductus ejaculatorius (Pl. 14, fig. 9, *e. j. d.*). Fig. 9 on Plate 14 shows the male generative organs magnified about four times linear, and considerably displaced to show the parts. The male also possesses a pair of male accessory glands, which extend as far forwards as the twenty-first pair of legs (fig. 9, *m. a. g.*).

The Female Generative System.—The female generative organs are typical of those of the species found in South America (Pl. 14, figs. 10 and 11). The ovary is small, and is attached to the floor of the pericardium in the region of the twenty-fifth pair of legs in specimens possessing twenty-eight pairs (fig. 10). The ova are small and endogenous. There is a pair of receptacula ovarum, the end sacs of which are small, and communicate with the funnel by a constricted neck (Pl. 14, fig. 11, *re. o.*). The receptacula seminis are well developed, oval in shape, and may be easily seen with the naked eye (fig. 11, *re. s.*). The uteri pass forward so as to form two ascending limbs, which on turning back form the descending ones, which end in an extremely short vagina (fig. 10, *ut.*). In the pregnant female the uteri contain embryos in all stages of development, ranging from the segmentation stages to young individuals possessing all the characters of the adult, save that they are lighter in colour.

SUMMARY OF CHARACTERS.

1. Six of the females are larger in size than the male.
2. The male specimen has twenty-four pairs of appendages.
3. One female has twenty-seven pairs of appendages, while the other seven have twenty-eight.
4. The renal apertures of the fourth and fifth pairs of legs

are placed on top of a papilla situated between the third and fourth spinous pads.

5. The papillæ situated near the mid-dorsal line are large, and stand on a base line which is almost rectangular. Principal papillæ alternate almost regularly with accessory papillæ. On the flanks the latter become broken up into several small ones, which occupy the spaces between the primary papillæ.

6. The female is possessed of receptacula seminis and ovarum.

7. The ova are small, devoid of yolk, and endogenous.

8. The embryos in the uteri are in successive stages of development.

9. The male has an elongated common duct, and on the twenty-second pair of legs has two pairs of sexual papillæ.

10. The outer blade of the jaw has one accessory tooth.

11. The inner blade of the jaw has one accessory tooth, followed by a diastema and a row of ten or eleven denticles.

CONCLUDING REMARKS.

On referring to Mr. Sedgwick's monograph on the Peripatidæ we find that he examined fourteen specimens collected by Mr. Sclater in the Pomeroon. Of these fourteen specimens he states that seven had thirty pairs of appendages, six had thirty-one, and one had twenty-seven. Out of thirteen embryos examined seven had thirty pairs and six had thirty-one. Of the four embryos taken from the one with twenty-seven pairs, three had twenty-seven and one had twenty-eight. In a foot-note, though not regarding it as probable, Mr. Sedgwick admits that the specimens with thirty pairs may be specifically distinct from those with twenty-seven and those with thirty-one.¹ In consequence of this uncertainty he included all the specimens under one specific

¹ "A Monograph on the Species and Distribution of the Genus *Peripatus* (Gülding)," 'Quart. Journ. Micr. Sci.,' vol. xxviii, N.S., pp. 431-494 pls. 34-40.

name, *Demeraranus*, though Mr. Sc Slater had previously given the same specimens (in part, at least) the name *im-Thurmi*.¹ If Mr. Sedgwick had followed a middle course, and had arrived at the conclusion that he had two species among the fourteen specimens which he examined, it would seem that he would have been nearer the truth than he was in the supposition that he might have three, or in the conclusion which he adopted, that he had only one. This view is supported by the following facts:—In the first place, out of the specimens possessing thirty or thirty-one pairs of appendages, Mr. Sedgwick obtained embryos with either thirty or thirty-one pairs, but out of the one with twenty-seven pairs he took embryos with either twenty-seven or twenty-eight pairs. In the second place, Mr. Sedgwick counted the number of appendages in no less than thirty-one specimens, both embryos and adults, and yet not a single specimen was found possessing twenty-nine pairs, which is a very curious fact if all the specimens belonged to one species. In the third place, all the fourteen specimens examined by Mr. Sedgwick were females, and consequently not likely to belong to one species. If the specimen with twenty-seven pairs of appendages had been a male, Mr. Sedgwick's view that he had only one species would not have been so improbable, as the males often have fewer appendages than the females. It may be fairly concluded that Mr. Sedgwick had among his fourteen specimens the representatives of two species; and, further, it is possible that if he had been writing his monograph to-day, instead of twenty years ago, he would have adopted a different view.

M. Bouvier,² in his review of the American *Peripatidæ*, does not raise the question here considered, and adopts Mr. Sc Slater's name (*im-Thurmi*) in preference to that of Mr. Sedgwick (*Demeraranus*).

¹ "On the Early Stages of the Development of a South American Species of *Peripatus*," 'Quart. Journ. Micr. Sci.,' vol. xxviii, pp. 343—361, pl. 24.

² 'Ann. de la Soc. Entomol. de France,' vol. lxxviii, 1899, pls. ii—viii.

That there are two species of *Peripatus* inhabiting the east bank of the river Demerara is an indubitable fact; namely, *P. guianensis*, with from twenty-four to twenty-eight pairs of walking appendages, and another species with thirty-one or thirty-two pairs. No males of the latter species having been discovered, it is impossible to say how many pairs of appendages they possess, but as regards the females it may be stated that, on an average, five out of every six have thirty-one pairs, the remaining one being provided with thirty-two. Although over sixty specimens were examined, the majority of which were young, born in captivity, not one of them was possessed of only thirty pairs of legs. If it be taken as proved that there are two species inhabiting the Pomeroon, the question whether these two species are respectively the same as those found on the east bank of the river Demerara immediately suggests itself.

In the first place, do the specimens with thirty-one or thirty-two pairs of appendages from the Demerara belong to the same species as those with thirty or thirty-one pairs brought from the Pomeroon and examined by Mr. Selater and by Mr. Sedgwick? This is a most difficult question to answer, as at present I have no material in hand from the Pomeroon. On the one hand, if we judge from the descriptions and figures given of *P. im-Thurmi*, we should have no hesitation whatever in answering this question in the affirmative; but, on the other hand, we must take into consideration the very significant fact of the discrepancy in the number of appendages. Among thirteen specimens of *P. im-Thurmi* examined by Mr. Sedgwick, seven had only thirty pairs of appendages, six had thirty-one, but none had thirty-two. Among sixty specimens from the Demerara examined by me fifty had thirty-one pairs of appendages, ten had thirty-two, but none had only thirty. In my opinion the complete lack of specimens with only thirty pairs of appendages from the Demerara, and of any with thirty-two pairs from the Pomeroon, are most significant facts, and incline me to believe that the animals under consideration form two distinct species.

In the second place, do the specimens with from twenty-four to twenty-eight pairs of appendages (*P. guianensis*) from the Demerara belong to the same species as the individual with twenty-seven pairs from the Pomeroon referred by Mr. Sedgwick to *P. demeraranus* (*P. im-Thurmi*, Sclater)? Although the supposition that the material from these two localities mentioned in the above question belongs to the same species seems legitimate, I do not consider it very probable. In discussing this question it should be remembered that Mr. Sedgwick saw Mr. Sclater's specimens alive, opened them, and took the embryos out of them; and although he was "unable to make a detailed examination of them in the fresh state," I am fully convinced that if the individual possessing only twenty-seven pairs of appendages had displayed the same characteristic markings as *P. guianensis* does, he would have immediately detected the difference between it and the remaining nineteen specimens of the collection in question. The most likely view seems to be that Mr. Sedgwick examined two species which could not be distinguished from each other with the naked eye, unless the appendages were counted a feature, to which, at that time, no great importance was attached. It is unfortunate that so little is known of the structure of the specimen possessing twenty-seven pairs of appendages from the Pomeroon, and the only correct attitude, until a further supply from that district shall have been collected, is to suspend judgment. Owing to this uncertainty I prefer using a new name, *guianensis*, to adopting the invalidated one, *demeraranus*, for the new species described in the present paper.

EXPLANATION OF PLATES 13 & 14,

Illustrating Mr. Richard Evans' paper on "*Peripatus guianensis* (sp. nov.)."

REFERENCE LETTERS.

ej. d. Ejaculatory duct. *m. a. g.* Male accessory gland. *m. d. l.* Mid-dorsal line. *ov.* Ovary. *p. p.* Primary papilla. *re. o.* Receptaculum ovarum. *re. s.* Receptaculum seminis. *s. p.* Secondary papilla. *ts.* Testis. *ut.* Uterus. *v. d.* Vas deferens. *v. s.* Vesicula seminalis.

PLATE 13.

The figure on this plate represents one of the biggest of the female specimens. It measured about 80 mm. in length when in motion.

PLATE 14.

FIG. 1.—This figure represents a portion of the skin situated on either side of the clear line which occupies the mid-dorsal position. The large primary papillæ (*p. p.*) alternate with the almost equally large secondary papillæ (*s. p.*). The apical piece of the primary papillæ is not represented. Note the tracheal openings situated on either side of the clear line and between the folds of the skin.

FIG. 2.—This figure represents a portion of the skin from a position close to one of the appendages. The primary papillæ (*p. p.*) lack the sharp basal outline of those shown in the first figure, and the secondary papillæ (*s. p.*) are far more numerous and smaller than those shown in the first figure, a result brought about probably by the breaking up of the latter.

FIG. 3.—This figure illustrates the inner blade of the jaw.

FIG. 4.—This figure illustrates the outer blade of the jaw.

FIG. 5.—This figure represents the fourth leg of the left side. Note the position of the renal papilla between the third and fourth spinous pads, and that it is quite clear of both of them.

FIG. 6.—This figure represents the twenty-second walking appendage on the right side of the male type specimen. Note the two large sexual papillæ situated on the postero-ventral aspect of the proximal end.

The fifth and sixth figures should be compared, because they incidentally

happen to illustrate the difference in appearance existing between a contracted and a non-contracted appendage.

FIG. 7.—This figure shows the structure of the foot. There are two primary papillæ on the anterior aspect, but only one on the posterior. On the ventral aspect there are two pairs of elevations, every elevation carrying three spines, which is the maximum number that was observed.

FIG. 8.—This figure shows a primary papilla from a position midway between the appendages and the mid-dorsal line.

FIG. 9.—This figure represents the posterior end of the male type specimen dissected from the ventral surface. It shows the male generative system, consisting of two tubular testes (*ts.*), two oval-shaped vesiculæ seminales (*v. s.*), two short vasa deferentia (*v. d.*), and a long and coiled ejaculatory duct (*ej. d.*), together with a pair of male accessory glands (*m. a. g.*).

FIG. 10.—This figure represents the posterior end of the female type specimen dissected from the ventral surface. It shows the female generative organs, consisting of an elongated ovary attached to the floor of the pericardium by a fine cord, receptacula seminis and ovarum, and two uteri (*ut.*), which contain young in different stages of development.

FIG. 11.—This figure illustrates the ovary (*ov.*), the receptacula ovarum (*re. o.*), the receptacula seminis (*re. s.*), and the commencement of the uteri (*ut.*) of the female.

Observations on Ovarian Ova and Follicles in
Certain Teleostean and Elasmobranch Fishes.

By

William Wallace, B.Sc.

With Plates 15—17.

INTRODUCTION.

THE ovaries of certain species of Teleostean and Elasmobranch fishes were examined with particular reference to the following points :

- (1) Post-embryonic origin of ova and follicular epithelium.
- (2) Yolk nuclei and their significance.
- (3) Egg-membranes and follicular epithelium.
- (4) Histology of egg-absorption.
- (5) Structural changes in ruptured follicles.

Before proceeding to consider these points in order, I shall give—(a) a brief general description of the peculiar ovary of *Zoarces*, based mainly on Stuhlmann's paper (1887); (b) some data bearing on the rate of growth and comparative fecundity of this species.

(a) Ovary of *Zoarces*.

Our knowledge of the anatomy, histology, and physiology of the ovary of *Zoarces* is due chiefly to Forchhammer (1819), Rathke (1824 and 1833), and Stuhlmann (1887).

The ovary of this species is of especial interest owing to the fact that it functions during about five months of every year of the adult animal's life as a uterus. In only one other "British" Teleostean, viz. *Sebastes marinus*, the Norway haddock, does a gestation of the young take place. The latter species is obtained by trawlers in rather deep water in the northern portion of the North Sea. *Zoarces*, on the other hand, is essentially a shore fish, commonly found in tidal pools, and apparently not going much beyond the laminarian region at any time. These two British viviparous fishes are not at all closely related. *Sebastes* is a Scorpaenoid, whereas *Zoarces*, while usually regarded as a blenny (viviparous blenny), has recently been relegated by Gill to the Anacanthine family, the Lycodidæ, and is classified accordingly in 'The Scandinavian Fishes' (1893).

The ovary of *Zoarces* is a single oval bag suspended by the mesovarium to the dorsal wall of the abdominal cavity. In the "resting" condition the organ is confined to the hinder third or so of this cavity. The oviduct is very short, and opens, in the adult, just behind the anus. When full of young the ovary extends forward in and almost fills the body-cavity, greatly distending the abdomen. The number of young of one gestation varies, generally speaking, from two or three to over a hundred,¹ in correspondence with the size and age of the mother. Although some amount of variation, local and individual, in the breeding season seems to obtain in *Zoarces*, there can be no doubt that the species as a whole breeds only once in the year, and bears its young in the depth of winter, as Willoughby observed.² The eggs are fertilised in August or September, and the young are born during the months of December, January, and February. At birth the young fishes are about 5 cm. or two inches long, and in general resemble the parent.

¹ Four hundred (Stuhlmann, 1887).

² See on this point Bambeke (1888), 'The Scandinavian Fishes,' part ii, p. 606; McIntosh and Masterman (1897), p. 218; 'Couch's Fishes,' vol. ii, p. 240.

Teleostean fishes have, as a rule, a pair of ovaries, and the single ovary of *Zoarces* has been shown by Jungersen (1889) to be the outcome of the fusion of paired primordia in the embryo. The testes are also paired in the embryo, and this condition is retained in the adult. Stuhlmann has described the arrangement of the ova on the internal surface of the ovarian wall. The eggs are not studded uniformly over the entire inner surface, but are limited to certain roughly longitudinal tracks, corresponding to low longitudinal lamellæ in the embryonic ovary. These lamellæ, which are conspicuous structures in many Teleostean ovaries, are suppressed in *Zoarces*, and are not obvious in the adult gland. The larger ova, however, instead of being sunk in the substance of the ovarian wall, are singly contained in vesicles or pouches which project from the wall of the ovary into its cavity. Each ovigerous pouch is a simple outgrowth of a portion of the wall, and its enlargement keeps pace with the growth of the contained ovum. The pouches which contain ripe or nearly ripe eggs are large pear-shaped vesicles about 4 mm. long and about 3 mm. broad. On the wide distal end of each is a cup-shaped depression, lined with a peculiarly modified epithelium. The epithelium consists of tailed cells, the tails resting on a basement membrane.

In the walls of each pouch is a network of blood-vessels. The vascular supply of these structures and its development have been described in detail by Stuhlmann (1887). It is important to observe that these ovigerous pouches are morphologically quite distinct from the ovigerous lamellæ of other Teleosteans.

Ovigerous lamellæ are longitudinal or transverse folds of the ovarian wall, and bear the germinal epithelium on their free margins (pipe-fishes) and often on their faces. Each lamella produces a great number of ova. In *Zoarces*, however, the lamellæ are suppressed, but each egg, as it grows, becomes carried out on a separate papilla of the ovarian wall. Not until the egg has attained a certain size

does it project beyond the general internal surface of the ovary. After the follicles in the ovigerous pouches have ruptured, and the ripe eggs have escaped, the pouches become drawn out into long clavate villi, whilst their vascular and connective tissues undergo considerable hypertrophy. The walls of the ovary at this time are hyperæmic, and the cavity contains an albuminous fluid. Red as well as white blood-corpuscles are present in this fluid, the former in great numbers. From these facts Stuhlmann inferred that, at the beginning of each gestation, the ovary passes into an inflamed condition, as a result of which an exudation from the blood of a nutritious albuminous fluid and a diapedesis of red blood-corpuscles takes place. The exciting cause of the inflammation is the retention in the ovary of the eggs and embryos, which then act as foreign bodies. In this way inflammation, which in general is a pathological phenomenon accompanying some specific disease, has, in the case of the ovary of *Zoarces*, become a normal periodic phenomenon, on the occurrence of which the maintenance of the species depends.

As to the function, if any, of the red blood-corpuscles in the metabolism of the fœtuses, Stuhlmann considers that the latter derive the oxygen for respiration from them. The corpuscles pass along with the nutritious albuminous fluid into the alimentary canal of the fœtus, and while, in Stuhlmann's judgment, the fluid is absorbed in the short small intestine, the red corpuscles are disintegrated in the enormously hypertrophied terminal portion of the gut, the rectum or "end-darm." The oxygen thus set free from the corpuscles is taken up by the blood-vessels in the walls of the rectum. This portion of the gut, therefore, functions as a kind of respiratory organ (!) (Stuhlmann, p. 42).

The histology of the general wall of the ovary is as follows:—The outermost layer is a single one of flat peritoneal epithelium. Next is a relatively thick coat of smooth muscles. In this layer run arterial blood-vessels, and also lymph-spaces lined with endothelium. The lymph-cavities

increase in size towards the inside of the ovarian wall. On account of the great development of these spaces the muscular coat is only attached by occasional strands to a relatively thin layer of stroma, containing venous blood-vessels and developing ova, that underlies the germinal epithelium.

(b) On the Reproduction of *Zoarcetes viviparus*.

There are given below, in tabular form, some particulars as to the rate of growth, age at first maturity, numbers of progeny, and relative numbers and size of the sexes of this species.

From Table I it is evident that at least some individuals attain sexual maturity at the end of their second year, dating from hatching (September).

TABLE I.

Date.	Number of specimens.	Range of length.	Average length.	Calculated approximate age. ¹	Condition of ovary.
May 5—10	7	cm. 5·5—7·2	6·5	8 months	A few larger ova, ·5 mm., becoming opaque.
June 5—24	21	7·2—8	7·5	9 months	
Sept. 4—30	10	8—11·7	10	1 year	
Females—Length.					
		cm.			
Feb. 24		13·2		1 year	Opaque ova up to ·9 mm.
June 14		14		5 months	
				1 year	Larger ova, ·9 mm., yolked,
				9 months	becoming translucent.
Sept. 15		13·3		2 years	Three embryos; one or two large aborted eggs.
Sept. 18		15·5		2 years	Eight embryos; five large aborted eggs.
Sept. 18		15·2		2 years	No embryos, but a set of large aborted ova.
May 15		19		2 years	Had had young previous season.
				8 months	

¹ Age calculated from September, when most of the larvæ are hatched.

TABLE II.

KIEL (Stuhlmann).				ST. ANDREWS.			OSTEND (Bambecke).			
Series.	Length of mothers.	Numbers of young.	Number of specimens.	Length.	Numbers of young.	Average number of young.	Number of specimens.	Length.	Numbers of young.	Average number of young.
(1)	cm.	—	3	13.3—15.5	3—8	—	9	cm. 12.5—14.5	12—37	—
(2)	—	—	—	—	—	—	12	15—16	17—45	—
(3)	17.5—21	Immature	9	16.5—21.5	12—29	21	7	17—21.5	23—62	40
(4)	22—23	30—40	4	22—23	24—32	28	5	22—23	71—103	85
(5)	25—30	50—180	8	24—29	37—96	5.2	8	23.5—26	41—155	93

TABLE III.

MALES.			FEMALES.		
Number of specimens.	Range of length.	Average length.	Number of specimens.	Range of length.	Average length.
28	12.5—27 cm.	19.2 cm.	45	13.3—29 cm.	20.4 cm.

In Table II the numbers of young, corresponding to a given length of parent, are compared in three localities. The numbers for Ostend and Kiel are taken from the papers of Bambeke (1888) and Stuhlmann (1887) respectively. Since the breeding season apparently synchronises at these three localities, the length measurements given are comparable. Well-marked local and possibly racial differences in respect of fecundity are apparent on inspecting this table. The average numbers of young, corresponding to a given length, are roughly about double at Ostend what they are at St. Andrews.

Table III gives the numbers and sizes of the sexes in a collection of adults, all of which were obtained at St. Andrews. The results confirm Willoughby's statement (Couch, p. 240) that "the males of this species are smaller in number than the females and of inferior size."

TABLE IV.

Length of mother.	Number of young.	Males.	Females.	Ratio of females to 100 males.
cm.				About
18	13	6	7	117
21	29	13	16	123
21	29	18	11	61
24	37	16	21	131
25·5	37	17	20	118
26·5	48	19	29	153

In Table IV the proportion of males and females in each of six broods is recorded. Females were in the majority in all cases but one.

Material.—The material for this work¹ consisted chiefly of post-embryonic ovaries of *Zoarces* in all stages of develop-

¹ The work on *Zoarces* was done at the Gatty Marine Laboratory, St. Andrews, during my tenure of a Berry Science Scholarship of the University

ment and degrees of ripeness. Observations were also made, mainly at Plymouth, on ovaries of the following species:—*Pleuronectes platessa*, *P. limanda*, *Sygnathus acus*, *Zeus faber*, *Salmo trutta*, *Spinax niger*, and *Chimæra monstrosa*.¹

Methods.—Only preserved material was employed in this research. The ovaries of *Zoarces* were, for the most part, fixed in Bles's fluid—a mixture of alcohol, formol, and acetic acid. The stains then used were borax carmine—either alone or in conjunction with picro-nigrosin—and hæmalum and eosin. Other material of *Zoarces*, after fixation in Hermann's platino-aceto-osmic mixture, was stained with thionin. Cytoplasmic and nuclear structures are brought out very sharply by stains after fixation in Bles's fluid.

The ovaries of *Spinax* and *Chimæra* were fixed in Bles's fluid, and stained either with borax-carmin and picro-nigrosin or with Heidenhain's iron-hæmatoxylin (long process) and orange G. The latter combination gave by far the most satisfactory results of any I have tried. Mann's methyl blue-eosin (1893) was also tried. By this method the red blood-corpuscles and the nucleoli of the germinal vesicle are the only structures to retain the eosin; the rest, nuclear reticulum, lanthanin, cytoplasm, etc., are all in various shades of blue and green. This result is rather surprising in view of Carnoy and Lebrun's conclusions ('*La Cellule*,' xii, xiv, xvi) in regard to the chemical nature of these nucleoli. These investigators hold it as proved that the nucleoli of the germinal vesicle in amphibians and fishes are parts of the chromatin or nuclein element. Since they contain a high

of St. Andrews. I have to thank Prof. McIntosh for suggesting the subject and for the kindly interest he took in the work.

While at Plymouth I held an 1851 Exhibition Research Scholarship. My thanks are due to the authorities of the Biological Station for granting me accommodation and ample supplies of material and reagents. I am under especial obligations to the Director, Dr. Allen.

¹ For the ovaries of *Spinax* and *Chimæra* I am much indebted to Mr. R. C. Punnett.

percentage of nucleic acid they stain with methyl green, the crucial test for chromatin. Methyl green is a notoriously difficult reagent to work with, and I was not successful in getting the nucleoli of teleostean ova to stain with it. With safranin, however, which is usually cited as a typical basic or chromatin dye, one can get the nucleoli to stain deeply or even exclusively if the washing-out process has gone far enough. The fact that the same nucleoli which show so decided a basophile or acid reaction when treated with methyl green or safranin are equally or even more prone to stain with eosin, a dye which is supposed to have quite opposite affinities, is not very easy to understand. The red blood-corpuscles are regarded as pre-eminentlly eosinophilous or acidophilous bodies. If, then, the reaction to eosin of these bodies can be used as a standard of comparison, then it is clear that the nucleoli of the germinal vesicle are strongly acidophilous, i. e. basic structures containing a high percentage of albumen or low percentage of phosphorus. We are thus led to contradictory results. One conclusion to be drawn from all this is that it is not always safe to make deductions in regard to the chemical nature of the various structures of the cell from a study of differentially stained sections of material which has been fixed in the ordinary liquids. If, on the other hand, we may rely on Mann's methyl blue-eosin method, the staining reactions certainly point to this. The microsomes of the germinal vesicle as they grow and become transformed into karyosomes or nucleoli undergo a chemical change, losing phosphorus or acquiring a larger proportion of albumen. Thus the change from blue to red is accounted for.

1. POST-EMBRYONIC ORIGIN OF OVA AND FOLLICULAR EPITHELIUM.

In foetuses of *Zoarces* 30 mm. long all the sex cells in the ovary were equal in size, and in a state of active karyokinetic

division; none of the ova had as yet entered upon their period of growth. In embryos 45 mm. long, however, permanent ova as large as .08 mm. in diameter were present. These ova had evidently been growing for some time, so that it is fair to assume that the ova for the first reproductive period commence to grow in the ovary of the foetal fish when the latter is between 30 mm. and 40 mm. long.

Observations mentioned above indicate that these first formed oogonia, or more correctly a certain proportion of them, ripen within two years, because certain if not all individuals of this species are mature at the end of their second year.

In post-embryonic ovaries of *Zoarces* oogonia are found either singly in the epithelium or collected into "nests" just below the epithelium. Such "nests" were found in ovaries of adolescent and adult females in the months of February, May, June, July, August, September, and October. In the month last named embryos were present in the ovary.

The oogonia and developing oocytes in *Zoarces* are localised in certain roughly longitudinal tracts of the inner surface of the ovary, "ovigerous lamellæ," found in so many other teleosts, being in this species suppressed. There is no obvious difference, in regard to the histological characters of the cells, between the epithelium covering the ovigerous tracts and that overlying the intermediate barren areas.

Where oogonia occur singly they are always found in the epithelium intercalated between the ordinary cells of this layer. At this stage the sex cells do not differ, so far as could be made out, from the epithelial cells, except in being slightly larger and rounded. The fact that the youngest sex cells (oogonia), when they occur singly, are never or rarely found anywhere but in the epithelium appears significant. On the hypothesis that the sex cells are formed once for all in the embryo, and never *de novo* in the ovary, one would expect occasionally to find single oogonia in the subjacent stroma, since, if these special cells are simply stored up in the ovary, there is no apparent reason why they should always be confined to the epithelium.

When we do find oogonia in the stroma they are aggregated into roundish balls, "nests" of karyokinetically dividing cells (figs. 1—5, 14, 15), in direct connection with the epithelium. From their compact rounded form the balls of oogonia have evidently been produced by the repeated division of a single mother cell. Further, the mother cell must have been situated in or just under the epithelium. One may, in fact, find all stages, from a single oogonium dividing into two whilst in the epithelium, to subepithelial collections of such, the "nests" just mentioned.

Closely wedged in amongst the oogonia of such a nest (fig. 1) are a number of small deeply staining nuclei. Some of these will form the follicular epithelium of subsequently developed oocytes (figs. 2, 3). The origin of these interstitial cells is somewhat difficult to make out. The nuclei of these cells are, on the whole, more like those of the ovarian epithelium than like the nuclei which occur in the stroma. Their chromatin, for one thing, is more pronounced. Figs. 4, 5, which represent portions of a section of a maturing ovary (February), show two "nests" formed entirely of follicular epithelial cells. The conditions here are very suggestive of an inward proliferation of cells of the ovarian epithelium. The absence of oogonia or oocytes in these particular "nests" may be accounted for by assuming either that the ova which were originally present have degenerated, or that none were formed, the proliferation inwards of the ovarian epithelium not being associated, as normally, with a transformation of certain elements into oogonia.

As to whether a fusion of oogonia normally occurs in connection with the formation of a permanent ovum or oocyte, I am inclined to think that this does take place, but that it does not involve the whole contents of a nest. The oogonia of a nest do not all fuse together to form a syncytium in which the nuclei multiply without corresponding division of the protoplasm, and from which a permanent ovum is subsequently separated in the manner described by Semper (1875) and Balfour (1878) in Elasmobranchs. Fig. 2 represents two

permanent ova developing in a single nest. In fig. 3 an ovum, further advanced, is shown. There can have been no extensive fusion here, since the permanent ova are still very small, while the outlines of the surplus oogonia are quite sharp and distinct. There was, however, frequently seen a fusion of oogonia with developing oocytes at a still earlier stage than that figured, before the formation of the follicular epithelium, and it is highly probable that the ovum passes through a sort of amœba stage, during which it ingests neighbouring oogonia, and grows in size at their expense. There was also observed a breaking down and fusion together of surplus oogonia in a nest to form a deeply staining granular mass, in which the original constituents are more or less entirely obliterated. Degenerate masses of this nature were sometimes, but not always, seen on the outside of a developing oocyte, somewhat flattened out between the latter and the epithelium. Sometimes, then, if not always, the unsuccessful oogonia go to the ground.

As to the nourishment of the developing oocyte, it seems probable after a very brief amœba stage is passed through, that this is supplied by the lymph through the follicular cells. As we have seen, the follicular epithelium is very early formed around the oocyte (fig. 2), and the successful ovum commonly occupies the deepest position in a nest (fig. 3) nearest the source of nutriment. Soon, by the disappearance of the unsuccessful oogonia, the oocyte comes to be surrounded on all sides but the outside by a lymph space, from which it is separated only by the follicular epithelium and a single layer of endothelium. A theca folliculi with blood-vessels is not formed until considerably later.

The above-recorded observations do not altogether bear out the views of Jungersen (1889), who has studied the origin of the ova in *Zoarces* and other forms. Jungersen found sex cells already differentiated in embryos of *Zoarces* 2 mm. long in which the blastopore was still open. He, and also Eigenmann (1896), have discarded the old notion of a

“germinal epithelium,”—that is to say, an epithelium covering or (Teleostei) lining the ovary, and possessing the theoretically unlimited power of giving rise to new oogonia by the transformation of certain of its cells in a way described by Balfour (1878) and many others. Jungersen, then, considers that ova are never formed *de novo* from the epithelial cells, neither does he derive the follicular epithelium from this layer, but from the stroma. An identical opinion is expressed by Eigenmann, who says, “There is no doubt concerning the continuity of the reproductive cells in *Cymatogaster*; they may be followed from very early conditions till sexual maturity without once losing their identity. No somatic cells are ever transformed into reproductive cells, and the comparative constancy of the latter up to 7 mm. makes it probable that none are ever changed into any other structures.”

The earlier accounts of the ova and follicular epithelium in Teleosteans differ, in some respects, from my own observations. Thus Brock (1881) thinks that the nests of primitive ova in *Perca* are formed by an immigration into the stroma of epithelial cells. He found in a nest all transitions from epithelial cells to the smallest primitive ova. Kollessnikov (1878) had previously described and figured for *Perca* an actual invagination of epithelium to form a “nest” after the manner of formation of a Pflüger’s tube in the mammalian ovary. In figs. 4 and 5 of the present paper a similar appearance is presented. Emery (1880) states that in *Fierasfer* the ovum originates from the germinal epithelium, and he figures a row of cells in the epithelium showing transition stages from ordinary epithelial cells to oogonia. He does not describe the formation of nests, nor is he able to say much as to the origin of the follicular epithelium. Stuhlmann (1887) says that in *Zoarces* the ova are formed from certain cells of the ovarian epithelium which sink into the stroma accompanied by neighbouring cells, and that the latter give rise to the follicular epithelium. Stuhlmann does not appear to have noticed particularly the formation of nests.

The evidence on this head at present available would seem to

point to the following as the most probable mode of formation of the ova and follicular epithelium in teleostean fishes. Ova and follicular epithelium have a common origin in the ovarian epithelium. The whole nest appears to arise by division of a single mother cell, some of the elements giving rise to oogonia, others to follicular cells. The successful oogonium ingests its immediate neighbours, and thereby increases to a certain size. Very early, however, the oocyte is surrounded by a complete follicular epithelium, the cells of which secrete fluid nutriment derived from the lymph. After formation of a permanent ovum and its follicular epithelium the surplus oogonia and follicular cells go to the ground.

2. YOLK NUCLEI.

A "yolk nucleus" of the type often noticed in invertebrate eggs,¹ and described particularly by Bambeke (1898) for *Pholcus phalangoides*, and by Calkins (1895) and Foot (1896) for earthworms, was met with in *Zoarces*. The complete history of this body in fishes does not appear to have been elucidated, although one finds allusions to an inner perinuclear zone of dark protoplasm by Scharff (1887), to numerous "Dotterkernen" in the cytoplasm of the egg of *Zoarces* by Stuhlmann (1887), to deeply staining granules "like nucleoli" outside the nucleus by Fulton (1898), etc. The body has been confounded and connected with another and quite distinct structure, the "centrosphere." It is to the latter, in fishes' eggs, that the name "vitelline nucleus" or "yolk nucleus" is usually but erroneously applied.

Figs. 6—13 and 37 illustrate the history of the true yolk

¹ Miss R. M. Clark, working at Plymouth, has kindly drawn my attention to the occurrence of a yolk nucleus of this type in the oocytes of *Flustrella hispida*. Her preparations and figures of developing ova show very clearly the same succession of appearances as I have figured and described for *Zoarces*.

nucleus. The first eight figures are drawn from ova of *Zoarces*, figs. 35, 36 from ova of *Sygnathus*, and fig. 37 from an egg of *Zeus faber*, the John Dory.

On its first appearance the yolk nucleus has the form of a cap of deeply staining substance applied to one side of the germinal vesicle. At this stage (fig. 6) it is very dense, almost homogeneous, and stains brightly with carmine. The yolk nucleus also stains deeply with hæmatoxylin and with methyl blue. As the egg grows the yolk nucleus becomes detached from the germinal vesicle, granular protoplasm intervening between the two (fig. 13). Vacuoles can now be seen in the yolk nucleus. With the further growth of the egg the following changes, as seen in figs. 7—13 and fig. 37, take place:—(a) The yolk nucleus gradually moves away from the germinal vesicle towards the periphery of the egg. (b) As it does so it alters its form, changing from a hemispherical or nearly hemispherical mass to a completely spherical shell, forming a distinct zone in the cytoplasm. (c) The yolk nucleus acquires a spongy structure, which gradually opens out during development. Later, the coarse threads of the sponge-work become disconnected with one another. The yolk nucleus breaks up into small pieces (fig. 10), the small pieces disintegrate into granules. Finally, amongst the dissolving granules are found the first minute oil drops (figs. 12, 37). (d) As the yolk nucleus moves away from the germinal vesicle it loses staining power, approximating more and more to the tone of the surrounding cytoplasm.

The changes in the yolk nucleus above described were followed in sections of material which had been fixed either in Bles's fluid, Hermann's fluid, formic-formol-alcohol, or picro-formalin. The yolk nucleus cannot be studied in preparations of material fixed in mixtures containing nitric acid, since the latter reagent dissolves it out completely. This may be seen at once on comparing fig. 35 with fig. 36. Both these figures represent a few ova near the edge of the germinal lamella in *Sygnathus*. The first figure shows

the effect of formic-formol-alcohol, the second illustrates the action of Perenyi's fluid. Such fluids as Perenyi's, Gilson's mercurio-nitric, and bichromate-osmic-nitric (Allen's) are therefore not suited to the study of the yolk nucleus.

The body in the ova of fishes which, following Cunningham (1897) and others, I take to be the centrosphere, is also indicated in the figs. 7, 8, 12, 21. It is a dense, round body, and, at a certain stage in the growth of the egg, is found in contact with the germinal vesicle (fig. 7), and then looks and stains very like a nucleolus. By this time the true yolk nucleus has attained some development. During the growth of the egg the "centrosphere," as we may provisionally call it, moves away from the germinal vesicle towards the surface of the egg. In *Zoarces* it degenerates in the zone of oil globules long before true yolk spheres appear. In the plaice it is last seen as a body, "recalling the form of an octopus" (Cunningham), with amœboid margin directed outwardly, in the zone of developing yolk spheres. In *Cymatogaster* it is said to remain over during the segmentation of the egg (Hubbard, Eigenmann). Stained with Mann's methyl blue-eosin the centrosphere is seen to be composed of two substances—a sponge-work staining purple, and contained in the meshes of this numerous granules, which stain red with eosin like the nucleoli.

As to the occurrence of the true yolk nucleus in teleostean fishes, I have observed it in the eggs of *Zoarces*, *Syngnathus*, *Salmo*, and *Zeus*, but I have not found it in the eggs of *Pleuronectes platessa* and *P. limanda*, although the latter were fixed in Bles's fluid and picro-formalin, just those reagents which were used to demonstrate the existence of this body in the other species. The "centrosphere," on the other hand, occurs in the ova of all species examined. It is most easily demonstrated in *Pleuronectes*, in which it is not obscured by a yolk nucleus.

Since the breaking up of the yolk nucleus is closely associated in time and space (see figs. 12, 37) with the first appearance of oil in the cytoplasm, and since the yolk

nucleus is conspicuous by its absence in the plaice and dab in the mature eggs, of which no oil spheres are present, it seems reasonable to conclude that there is some functional relation between this peculiar substance and the oil. What is the precise chemical relation between the two it is impossible, at the present stage, to say. In general, fat is a product of the decomposition of proteid substance, as exemplified in the phenomena of fatty degeneration. A special case of fatty degeneration of protoplasm will be mentioned below when dealing with the absorption of ova in fishes.

That the activity of the germinal vesicle is associated with the production of oil in the cytoplasm seems to be indicated by the fact that it also is a centre of formation of oil droplets. The oil drops peripherally situated on the site of the "yolk nucleus" are, however, the first to appear (fig. 37). It is certain, on the other hand, that the nucleoli are not transformed either into oil globules or yolk spherules, as Calderwood (1891) and Scharff (1887) supposed. In all probability the membrane of the germinal vesicle is, as Carnoy and Lebrun have stated, imperforate, so that no transmission of solid material but only osmosis can take place through it.

I have not been able to follow with certainty the "centrosphere" in oocytes younger than the stage represented in fig. 7. I observed, however, under moderately high powers (Zeiss D, ocular 4) the karyokinetic division of oogonia in *Zoarces*. The preparations were fixed in Bles's fluid and stained in bulk with hæmalum. I have not been able to follow the details of the process owing to the extremely small size of the oogonia (figs. 14, 15).

In *Lumbricus*, according to Calkins (1895), the yolk nucleus first appears as an irregular deeply-staining body, which is closely applied to one end of the germinal vesicle, its substance being connected with the interior of the latter. It ultimately breaks up into small bodies scattered in the cytoplasm.

Katharine Foote (1896) states that in *Allolobophora*
VOL. 47, PART 2.—NEW SERIES.

fœtida, an earthworm, the "so-called yolk nucleus" first appears as a granular mass in the form of a crescent in intimate contact with the nucleus of the egg. "This substance greatly increases as the egg grows." According to this observer the destiny of the yolk nucleus, which she regards as consisting of archoplasm, is to form the "polar rings" at maturation. This is certainly not the fate of the yolk nucleus in teleostean fishes.

Bambeke (1898) gives an elaborate and beautifully illustrated account of the history of the "corps vitellin" in *Pholcus phalangoides*. Here, again, as in the earthworms and in *Zoarces*, the body in question first appears as a crescentic mass fitting over one side of the germinal vesicle, and, as the egg grows, the corps vitellin becomes circular and moves away towards the periphery, where it breaks up into separate fragments, and finally into "granules safraninophiles." The latter are then metamorphosed into "éléments gras," while about the same time the first (proteid) yolk-spheres make their appearance.

The above-recorded observations on *Zoarces* agree very closely with Bambeke's description. I think there can be little doubt as to a relation of some sort of the yolk nucleus substance with the formation of oil in the egg cell. Whether the oil is in any way related to the production of proteid yolk spheres is uncertain. The fact that in ovarian eggs of the plaice, dab, and some other fishes there are no oil drops (Cunningham, 1897), seems proof that oil is not a necessary stage in the series of chemical changes leading to the production of yolk spheres in the egg. Again, as demonstrated by Cunningham (1897) and Fulton (1898), oil globules make their appearance in ovarian eggs of fishes long before the yolk spheres. What I have seen in *Zoarces* and *Sygnathus* confirms this. The yolk spheres do not make their appearance until the approach of the spawning period, and they are deposited, at first peripherally, as fine granules in the protoplasm intervening between the oil globules.

That the roundish body in the cytoplasm—that which is

usually characterised as the "yolk nucleus" in fishes, but which is probably the centrosphere—has any connection with the formation of yolk seems improbable, if we consider that it may degenerate at very different times in different species.

3. EGG MEMBRANES AND FOLLICULAR EPITHELIUM. ^v

In regard to egg membranes it is of most interest and importance to know—(1) whether they are formed from the follicular epithelium or at the expense of the egg itself; (2) if they are of the nature of secretions, or are produced by a metamorphosis of living protoplasmic substance; (3) what are the homologies subsisting between the various membranes found in different groups of vertebrates? (4) is there a living protoplasmic connection between the cytoplasm of the egg and that of the cells of the follicular epithelium by means of which nutrient substances secreted by these cells might pass into the egg? The question whether the deutoplasm is manufactured by the egg itself or in the cells of the follicular epithelium naturally suggests itself in this connection.

It will be well, before referring to some observations of my own on this head, to make a brief statement of the chief opinions of the more recent workers. Perhaps the two most important papers of comparatively recent date on the structure and development of egg membranes in fishes are those of Mark (1890) and Eigenmann (1890). Since the first-mentioned observer gives a critical review of all the previous literature on the subject of egg membranes, it is unnecessary to attempt anything of the kind here.

Classification of Egg Membranes.—Mark recognises four kinds of egg membranes in fishes:

(1) The innermost: a true vitelline membrane, representing the cell membrane of the egg. Its existence has been demonstrated by Scharff (1887), Fulton (1898), and others in the ripe ovarian ova of certain teleostean fishes. On

applying gentle pressure to the egg the "zona" ruptures, and the vitellus tightly clothed with the fine homogeneous vitelline membrane protrudes through the fissure thus produced.

(2) Zona radiata,
(3) Villous layer (Lepidosteus), } produced by the ovum.

(4) Müller's capsular membrane in the perch and pike—a product of the granulosa or follicular epithelium.

Eigenmann gives the following classification :

(1) Eggs with single membrane. The zona radiata: *a*. Zona a single layer of uniform structure; *b*. Zona differentiated into an outer and inner layer.

✓ (2) Eggs with a zona radiata and a thin homogeneous outer layer. The outer membrane may bear appendages.

(3) Eggs with a zona and a thick outer layer produced by secretion of the granulosa cells.

In addition to all these a "zonoid" membrane has been described. It was discovered in the eggs of teleosts by His, and subsequently observed by Emery (1880), Scharff (1887), Eigenmann (1890), and others. It underlies the zona, and according to Scharff, who found it in the immature ovarian ova of the gurnard, is "semi-fluid, usually devoid of granules, and stains only slightly." In ripe ova it disappears entirely. The zona is formed before the zonoid layer. In *Blennius pholis* there is no zonoid layer (?).

In Elasmobranchs the number of egg membranes appears from the observations of Balfour (1878), Giacomini (1896), and others to be constant, viz. two. These are an outer homogeneous one, named by Balfour the "vitelline membrane"—though quite distinct from the true vitelline membrane above mentioned,—and an inner radially striated one, the "zona radiata." Beddard observed two apparently homologous membranes in the ova of Dipnoi. Emery (1880) draws attention to the similarity of the zonoid layer in *Fierasfer* to the zona radiata of Balfour. Scharff, again, identifies the zonoid layer in the gurnard with Beddard's zona radiata.

Origin of Egg Membranes.—This point has been the subject of much discussion. The general consensus of opinion seems to be in favour of the view that, with certain exceptions, such as the capsular layer in the perch, the egg membranes are derived from the egg itself, being cuticle-like secretion therefrom. Balfour maintained that the vitelline membrane of *Raia* and *Scyllium* was no less than the zona radiata the product of the egg; that in some cases the vitelline membrane was formed before the egg possessed a distinct follicular epithelium. Schultze (1875), however, held the opposite view. Van Beneden's observation (1880) on the bat seems to prove that the zona pellucida (zona radiata) is or can be formed without the intervention of the follicular epithelium. Van Beneden frequently observed that where two or more ovarian ova were in contact over a considerable area the zona pellucida was as thick at the places where the eggs touched as at those regions where they were invested with the follicular epithelium.

Mark discusses exhaustively the origin of the egg membranes in *Lepidosteus*. In this species there are two, an outer and an inner, called by Mark the villous layer and zona radiata respectively. The villous layer is the thicker, and is composed of closely set villi, radially arranged with reference to the centre of the egg. "Each granulosa cell corresponds in number to four to eight villi, but there is no constancy in the position of the cells or their nuclei in reference to the underlying villi." From various evidence, Mark is "certain that the layer which is first to make its appearance between the yolk and the follicular epithelium is the villous layer;" and that, like the zona radiata, the villous layer of the egg membranes in *Lepidosteus* is also the product of the ovum itself rather than of the follicular epithelium surrounding it." Further, Mark has clearly demonstrated the existence of pore canals in the zona radiata of *Lepidosteus*, and has shown that the villi of the villous layer are rooted in these canals.

A morphologically quite distinct structure is the capsular membrane of the perch. This, according to Mark and

Eigenmann, is the product of the follicular epithelium, and the tubules which it contains are filled with processes of the follicular cells. Previously Brock (1878) had thus described this membrane:—"The follicular cells, which are at first in close contact with the young egg, are raised up from the zona radiata by the developing gelatinous layer, and, with the advancing growth of that layer, are drawn out into long processes, which can be followed up to the zona." According to Mark, "the process by which the capsular membrane is formed is neither simply a cell secretion nor exclusively a cell metamorphosis." I have come to a similar conclusion in regard to the egg membrane of *Chimæra* (fig. 30). This figure may be compared with Brock and Mark's description of the capsular membrane of the perch.

Another example of an egg membrane formed from the follicular epithelial cells is, according to Eigenmann, the outermost thin homogeneous membrane, with or without appendages, found in *Fundulus*, *Pygosteus*, *Clupea vernalis*, etc. In regard to *C. vernalis*, Eigenmann says, "This outer membrane is intimately connected with the granulosa cells, so that it usually retains its connection with the granulosa when the latter is artificially separated from the zona. In all cases slender striations extend from it to the zona radiata." I have found in *Zeus faber* a membrane which seems to answer very well to this description (fig. 34).

Eigenmann considers that the zonoid layer, seen by him in immature eggs of *Amiurus*, is an artificial product, due to the contracting effects of reagents employed in preparing the ova for sections. The characteristic appearance of the zonoid layer—that of radially arranged fibrils underneath the zona—is caused "by the partial withdrawal of the protoplasm occupying the pore canals of the zona." "Such an origin of the zonoid layer would," he says, "also explain its disappearance in ripe eggs. After the egg has attained its full size the connection of the yolk with the substance in the canals would naturally be less intimate than at an earlier

date, and then the contraction of the yolk would not be accompanied by the stretching of any filaments across the space thus produced."

Reasons will be given below for regarding this view as to the origin of the zonoid layer as incorrect.

Nutrition of the Egg by the Cells of the Follicular Epithelium.—It has been demonstrated in the case of *Talpa* by Heape (1886), and in *Echidna* by Caldwell (1887), that the zona pellucida is perforated by protoplasmic processes connecting the protoplasm of the ovum with that of the follicular epithelium. Eimer (1872) found the same condition in the ovarian ova of reptiles. Balfour (1878), although he observed that the cells of the follicular epithelium in *Raia* and *Scyllium*, after being teased out in osmic acid, had slender processes attached to them, was not able to say that these had passed through the homogeneous "vitelline membrane." In the ovarian ova of Teleosteans Fulton (1898) thinks that the existence of radial pores in the zona is unproved.

Eigenmann (1890), on the other hand, considers that their presence is well authenticated. He says, "The meaning of the pore canals in the intra-ovarian egg, at least, needs little discussion. In most of the sections prepared, where the granulosa cells are slightly raised from the zona radiata, processes of the granulosa cells can be seen to enter the pore canals." So far as I know, neither in teleostean nor in elasmobranch fishes have processes of the follicular cells been seen actually to traverse the substance of the egg membrane. In *Chimæra*, however, they can be clearly seen to do so (fig. 30).

Gegenbaur, Balfour (1878), Van Beneden (1880), and others were of the opinion that the deutoplasm is manufactured by the egg itself, and is not derived from the cells of the follicular epithelium. This is proved by the following facts—which hold, at any rate, for Teleosteans and Elasmobranchs:—(1) The yolk particles are first formed at some distance in from the surface of the egg. The cortical layer

of egg protoplasm is free of yolk. (2) No yolk granules are ever found in the cells of the follicular epithelium unless the egg is undergoing absorption through the action of these cells. In the normal follicle, while deposition of yolk is going on in the egg, no granules are seen in the follicular cells.

Caldwell (1887), speaking of the ovarian egg of *Echidna*, states that "food material is formed in cells of the follicular epithelium as well as in the ovum itself, and appears first as minute granules in the neighbourhood of the nuclei and germinal vesicle, and every stage is to be found, from the most minute granules up to the largest yolk spheres of the mature ovum. From the nucleus of each follicular cell, and from the germinal vesicle, streams of these yolk granules travel into the body of the ovum. Further, "the streams of yolk granules passing into the ovum, immediately on entering, are more or less parallel to each other, and give a radially striated appearance to the peripheral layer of the ovum. A similar appearance in other vertebrate eggs has been described as a definite membrane, and named the *zona radiata*." This is doubtless the *zonoid* layer again. If so, I cannot agree with Caldwell's explanation of it. The above observations of Caldwell on the nutrition of the egg in *Echidna* were, it is necessary to remember, made on fixed, stained, and sectioned ova.

In fig. 18 the investments of a nearly ripe ovum of *Zoarces* are shown in section. The material sectioned had been previously fixed in Bles's fluid and then stained with borax carmine and picro-nigrosin. The section is that of an almost ripe egg 2.5 mm. in diameter. The egg membrane measured .004 mm. in thickness. The follicular epithelium is separated on the outside from the *theca folliculi* by a fine homogeneous membrane, the *membrana propria folliculi*. The follicular epithelium consists of a single layer of flat cells with elliptical nuclei. These nuclei lie with their long axes parallel to the surface of the egg. The cells repose directly upon the outer surface of the egg membrane, and the latter

rests immediately on the surface of the yolk (*vt.*). In the egg under consideration most of the yolk spheres have flowed together into a single mass occupying the bulk of the egg. Only in the cortical protoplasmic layer are separate spheres and oil globules still to be found. In this preparation the egg membrane appears to be homogeneous, but in other sections there are indications of a fibrillar structure. On surface view the membrane is distinctly punctate.

Fig. 17 represents an earlier condition of the egg membranes, etc. This figure was drawn from a section of an egg .5 mm. in diameter, in which numerous oil globules but no yolk spheres were present. Here the follicular epithelium, as before, is a single layer of cells. The egg membrane (*z.*) is very thin, no thicker than the membrana propria, and reposes on a peculiar layer consisting of cytoplasmic threads closely set and radially arranged with reference to the centre of the egg. The spaces between the threads do not appear to contain any substance. If any substance is present it is structureless, unstainable, and therefore invisible. This layer is the zonoid layer observed by His, Scharff (1887), and others in various teleostean ova. At this stage the zonoid layer is clearly delimited from the subjacent cytoplasm by what appears as a rather thin line under moderate powers of the microscope; it is probably caused by a condensation and parallel arrangement of cytoplasmic trabeculae. In still smaller eggs, in which the protoplasm is denser and more compact, the radial fibrils composing the zonoid layer are still more closely arranged, and are directly continuous with those of the general network; that is to say, there is no line of separation on the side of the vitellus, the zonoid layer appearing rather as a differentiation of the superficial protoplasm. On the side of the egg membrane the zonoid layer is likewise bounded by a thin surface distinct from the inner boundary of the egg membrane proper, but this can only be seen in sections in which, owing to the contracting effects of reagents, the zonoid layer has parted from the egg membrane proper.

We see, therefore, that immature ova, as compared with ripe eggs of *Zoarces*, possess an extra membrane, the zonoid layer; that this layer arises as a differentiation of the superficial protoplasm; that it becomes distinct from the vitellus, and then consists of radial fibrils supported above and below by thin surfaces—quite separate from either the vitellus or the egg membrane proper; that is to say, it is now a distinct layer. It follows from this, and from the obvious fact that the radial fibrils are far more numerous than the cells of the follicular epithelium, that the zonoid layer cannot be “due to the partial withdrawal, through contraction, of the protoplasm occupying the pore canals of the egg membrane,” as Eigenmann supposed. It is to be carefully distinguished from a true egg membrane, because, so far as can be made out from microscopic examination, it is a “living” membrane, the fibrils of cytoplasm of which it is composed not having undergone any chemical metamorphosis, nor apparently do the spaces between the fibrils contain any substance. The zonoid layer seems to disappear in the ripe egg. My own impression is that during the great and rapid increase in the volume of the egg at maturation the zonoid layer is stretched out under the egg membrane, and is so attenuated as to be invisible in ordinary preparations.

Identical appearances were seen in surface sections of immature ova of *Sygnathus acus*, *Salmo Levenensis*,¹ and *Pleuronectes platessa*. The eggs of these four species—and no doubt of many other Teleosteans—possess a single definitive egg membrane or zona radiata, while below this, in immature ova, is the zonoid layer. I think these eggs should all be placed in Eigenmann’s first category, i. e. “(1) *a*. Zona a single layer of uniform structure.”

— The investments of the ovarian egg of the John Dory—*Zeus faber* (fig. 34)—are thicker and more complex. There are three distinct membranes, or, if we include the zonoid layer, which is, as usual, present in the immature

¹ I have to thank Dr. H. M. Kyle for the ovary of the Loch Leven trout.

eggs, there are four.¹ The outermost, in eggs about .33 mm. in diameter, is a very thin, homogeneous, deeply staining membrane, to which the follicular epithelial cells are closely applied. It appears to me to answer to Eigenmann's description of the outer membrane in *Clupea vernalis*. Certainly, where this membrane is raised up from those underlying it, "slender striations are seen to extend to the zona radiata." The appearance and relative thickness of the underlying membranes are shown in fig. 34. The second outer membrane is by far the thickest in ovarian eggs at this stage; it is roughly about three times as thick as the next inner membrane. The zonoid layer (*p. v. l.*) is present as usual.

The egg membranes in *Zeus* develop in succession from without inwards. The fine homogeneous outer membrane is formed first, but whether by the egg or by the follicular cells could not be determined. The difficulty of the determination lies in the circumstance that the follicular epithelium is present around the egg from a very early stage. Once the outer membrane is formed, the others arise in succession from the cortex of the egg. The manner in which they arise from the cytoplasm of the egg was not followed with high powers, but so far as could be made out each membrane at its first appearance resembles the zonoid layer (*p. v. l.*), and is later metamorphosed into a true zona. The definitive zonoid layer is the last to form, and remains in the "living" condition. It may, however, be regarded as a potential egg membrane. The regular radial arrangement of its protoplasmic fibrils, along which the nutrient secretion of the follicular cells must pass, perhaps facilitates the equal and symmetrical distribution of food material in the egg.

Gathy's account (1900) of the mode of origin of the egg membranes in *Clepsine complanata* appears to me to

¹ Fulton (1898) mentions the thick "double" capsule of the ovarian egg of *Zeus*, and adduces the condition as indicating the probable demersal character of the ripe egg. Fulton does not appear to have noticed either the extremely fine outermost membrane, or the zonoid layer.

represent most accurately what takes place at the surface of the egg. His figs. 42, 43 speak for themselves, but his concise description may advantageously be quoted here. He says ('La Cellule,' xvii, p. 47), "La membrane de l'œuf est d'abord simple, et formée d'une seule couche visible, à laquelle aboutissent les trabécules du réticulum cytoplasmatique. Cette membrane, très fine au début, s'épaissit dans le cours du développement de l'œuf; de nouvelles couches s'ajoutent progressivement de dehors en dedans. À cet effet les trabécules se régularisent sous la membrane; les unes s'ordonnent radialement les autres s'orientent perpendiculairement à celles-ci de façon à former une strie concentrique bien régulière. Cette strie d'abord assez éloignée des couches préexistantes, s'en rapproche de plus en plus et devient partu intégrante de la membrane."

Turning now to Elasmobranchs, we find in *Spinax* and *Chimæra* apparently the same two membranes that we met with in *Zoarces*, etc., viz. the zona and the zonoid layer. I refer, of course, to the immature eggs, for, as Balfour (1878) has shown, the membranes (in *Scyllium* and *Raia*) are absorbed before the ovum quits the follicle. It happens that in fig. 19, which represents a section at the surface of an immature egg of *Spinax*, the zonoid layer is not clearly seen. The hardening action of reagents and the subsequent strain of osmosis on the hardened structures have caused the vitellus to separate from the zonoid layer, which has in turn greatly contracted, so as to be scarcely visible at this particular point. In other parts, however, of the same egg the zonoid layer can be distinctly seen; it is perfectly constant in *Spinax* and in *Chimæra* (figs. 29, 30), and has the same properties as in *Zoarces*.

The portion of the section drawn in fig. 19 was specially selected because it shows the relation of the cells of the follicular epithelium to the egg membrane. As a result of the contracting effect of reagents, the follicular epithelium is raised up from the egg membrane, and its cells are seen to be provided with delicate processes, the distal ends of which

are fixed in the membrane. In other sections, again, the vitellus, together with the zonoid layer, has shrunk away from the egg membrane, while the follicular epithelium is closely applied to the latter. At such places delicate fibrils may occasionally be seen stretching across the space, to be inserted in the egg membrane. Although no processes were seen actually to traverse the substance of the egg membrane, it is difficult to account for the appearances just described except on the assumption that the membrane is penetrated by the processes of the follicular cells. In *Chimæra* the demonstration of processes of these cells traversing the (modified) egg membrane is complete (fig. 30).

Chimæra differs from *Spinax* in regard to the condition of the follicular epithelium in immature egg. In *Spinax* the follicular epithelium is a single layer of cells, flat in the smaller eggs and over the animal pole of the larger ova, but more or less columnar over the rest of the surface, and especially high at the vegetable pole (fig. 19). *Spinax* resembles *Acanthias vulgaris*, *Scymnus lichia*, *Heptanchus cinereus*, and *Mustelus lævis*¹ in the persistent single-layered condition of the follicular epithelium. *Chimæra* agrees with *Raia*, *Scyllium* (Balfour), *Torpedo* (Schultze), *Myliobatis*, *Trygon* (Giacomini), in having a thick follicular epithelium with two kinds of cells—large specialised “nutritive” cells and small indifferent cells. The same differentiation of the cells in the follicular epithelium is found in reptiles. The nutritive cells degenerate and disappear before the maturation of the egg, when the follicular epithelium reverts to the single-layered condition.

Giacomini (1896) gives a brief description of the follicle of *Chimæra*. He mentions that the epithelium consists of large cells, intercalated among which are small cylindrical cells; that the large cells possess a vesicular nucleus; that they are provided with fine processes directed against the vitelline membrane.

In the very young follicles of *Chimæra* the follicular epi-

¹ Giacomini, 1896, p. 230. *Spinax* was not investigated by this author.

thelium is a single layer of small uniform cells as in all other species. The large nutritive cells make their appearance at a very early stage in the development of the follicle (fig. 28). In this case it is not easy to say whether we have two oocytes in a follicle, one of which—to the left—has taken the lead, or whether the large cell to the right of the figure is a nutritive cell derived from the follicular epithelium. The resemblance to oocytes of these large nutritive cells is very striking, and suggests interesting considerations. Semper went so far as to say that the larger cells in such follicles were probably primitive ova destined to become permanent ova. Schultze (1875) thought the large cells in the follicular epithelium of *Torpedo* were leucocytes.

Figs. 29 and 30 are sections of the follicular epithelium and adjacent structures in *Chimæra monstrosa*. Fig. 30 shows the condition of the epithelium and egg membrane towards the vegetable pole. Fig. 29 is a section nearer the animal pole. This distinction between animal and vegetable poles becomes well marked, both in *Spinax* and *Chimæra*, at a very early period in the growth of the oocytes, and is initiated by the migration of the germinal vesicle to one end of the egg. I have noticed in both species that it is invariably to the same side that the nucleus travels, viz. to that end which is diametrically opposite to the area of attachment of the egg to the surface of the ovary. In other words, the animal pole is always directed inwards, towards the substance of the ovary. Whether the direction of migration of the germinal vesicle has any relation to the source of nutrient supply I cannot definitely say, but it is worth remarking that in the substance of the ovary both of *Spinax* and *Chimæra* there is a great development of lymph spaces. Further, each follicle is surrounded by a lymph space, except on the side where the follicle is attached to the ovarian wall. It may be that the nucleus travels to that side which is most favourably situated for access to the lymph.

The polarity of the egg in *Spinax* and *Chimæra* is also manifested in the difference in the condition of the follicular

epithelium and egg membranes at the two poles. This difference is especially striking in *Chimæra*. Figs. 29 and 30 do not by any means represent the extreme conditions. The follicular epithelium is very much flatter, and the egg membrane very much thinner over the place where the nucleus is situated than is represented in fig. 29, a section from the side of the egg, nearer the animal pole, but some distance from it. As we pass towards the vegetable pole the egg membrane gradually becomes thicker, and at the same time laxer in structure, until, as in fig. 30, it presents an appearance as if it had been teased out and resolved into its component fibres. As we travel over the surface of the egg towards the animal pole we see how the egg membrane is constituted, viz. by a matting together and condensation of fibrils at the surface of the egg.

Figs. 29 and 30 are both drawn to the same scale, so that the thickness of the follicular epithelium and egg membrane in the one figure may be directly compared with their thickness in the other. We then see that corresponding with a greater thickness and laxer structure of the egg membrane is the greater depth and laxer arrangement of the follicular epithelium. As we approach the vegetable pole of the egg the processes of the follicular cells, which can be distinctly seen to pass through the egg membrane, become more obvious. As the membrane thickens the processes lengthen, and we get the condition shown in fig. 30. The processes can often be seen to take a spiral course through the mass of fibres composing the egg membrane. In iron hæmatoxylin-orange preparations these fibres stain with the orange like the fibres of connective tissue. Their course is, for the most part, radial with respect to the centre of the egg, but they seem to branch and anastomose with one another. Although in many cases apparently living protoplasm, granular and staining with hæmatoxylin, can be traced right through from a follicular cell to the zonoid layer, in other cases the processes of the follicular cells pass insensibly into the substance of certain of the fibres. I cannot say whether there is a gelatinous sub-

stance in the spaces between the fibrils of the egg membrane. If so, then this substance does not stain either with carmine, orange-hæmatoxylin, or picro-nigrosin.

The above observations on the condition of the follicular epithelium and egg membrane in *Chimæra* point to the following conclusions:—(1) The egg membrane is formed, in part at least, at the expense of the cells of the follicular epithelium. This is indicated, although not by any means proved, by the fact that where the follicular epithelium is thickest and has greatest number of cells per unit area, the egg membrane is also thickest; and where the follicular cells are fewer and more densely arranged, the egg membrane is thinner and denser. (2) Processes of the follicular cells pass through the egg membrane to its inner limit. Granular matter—stained with hæmatoxylin—can be traced through the fibrils of the zonoid layer to the yolk. The appearance of the peripheral portion of the vitellus is roughly indicated in the figs. 29 and 30. Radiating masses of granules, darker than those of the general cytoplasm of the egg, extend into and become lost in the latter.

The most remarkable feature about the *Chimæra* follicle is the great thickness of the follicular epithelium and differentiation of its cells above alluded to. The arrangement of these cells is very characteristic. The smaller uniform cells form an outer layer next the *membrana propria*, but extend in wedge-shaped masses between the large specialised nutritive cells. Transitions between the two kinds of cells can be found frequently, although there were never seen any indications of karyokinesis in the large cells. No doubt the ranks of the nutritive cells are renewed from time to time from the small generalised cells.

Summary.—(1) In immature ova of the teleostean and elasmobranch species examined, the cytoplasm of the egg is differentiated at its surface into a perivitelline or zonoid layer of peculiar structure, consisting of closely set, radially arranged protoplasmic fibrils. These fibrils are at first connected with those of the general cytoplasmic reticulum,

but later the zonoid layer is marked off as a distinct membrane. The zonoid layer is identical with Balfour's *zona radiata*.

(2) The origin of the definitive egg membrane (*zona radiata*) in *Zoarces*, and other teleostean species, and of the outermost membrane in *Zeus* was not ascertained. The egg membranes of *Zeus*, with the possible exception of this outer layer, are derived from the protoplasm of the ovum apparently by a matting together and subsequent chemical metamorphosis of cytoplasmic fibrils somewhat as Gathy has shown for *Clepsine*.

(3) The egg membrane of *Chimæra* appears to be intimately connected with the follicular epithelium, and is probably formed—in part at least—at the expense of this layer.

(4) In *Spinax* and *Chimæra* the cells of the follicular epithelium are provided with delicate processes, which penetrate the egg membrane and convey nutriment to the egg.

4. HISTOLOGY OF EGG ABSORPTION.

The details of the histological changes which accompany the degeneration and absorption of ova have been studied chiefly by Brunn (1882) in birds, and Ruge (1887) in amphibia. Of those who have worked at the structure of the teleostean ovary, few have failed to notice the obvious fact that a certain proportion of the ova come to nothing, but undergo a fatty degeneration. The degeneration of ovarian ova in fishes is mentioned by His (1873), Brock (1878), Emery (1880), Owsianikov (1885), Barfurth (1886), Cunningham (1897), and other writers.

An immigration into the substance of the degenerating egg of foreign elements, usually described as cells or nuclei, has also been noted by various observers, and has been variously interpreted. The earlier attempts to explain this occurrence of intra-vitelline nuclei or cells were very wide of the mark.

Barfurth gives an account of the degeneration of ova in

the trout. It seems that in this species sometimes the whole batch of ripening ova for one spawning are reabsorbed. Consequently, at the breeding season, a certain proportion of the females are unripe; not because they have not reached that age at which sexual maturity is attained, but on account of the retention of the season's ova. For some reason, at present obscure, the dehiscence of the follicles containing these eggs had not been brought about. These unspawned ova then undergo fatty degeneration. Further, according to Barfurth (1886), the presence in the ovary of these inert degenerate masses may hinder the production of ova for the next spawning period. Accordingly the unripe condition of certain individuals may last for two years or more. To what extent this phenomenon, viz. the reabsorption of an entire crop of ripening ova, is prevalent in Teleosteans is unknown. One specimen of *Zoarces* was found in this condition at the breeding season on September 18th, 1901. Another is mentioned by Stuhlmann (1887, p. 33).

In regard to the histology of egg absorption, Barfurth states that a growth and perhaps a proliferation of follicular epithelial cells, and an immigration of these cells into the interior of the egg, accompany the degeneration of the latter. Barfurth considers that leucocytes play only a subordinate part in the process of reabsorption. His figures show what are apparently initial stages. In one figure (fig. 12) the germinal vesicle is absent, and a few round dark bodies, which may be cellular or nuclear, are embedded about the centre of the yolk. In the figure of another egg (fig. 15) the follicular epithelium around the egg is thicker, and contains fat drops.

Stuhlmann (1887, p. 20) observed that in immature ovaries of *Zoarces* certain of the follicles contained, in place of an egg, a "Zelldetritus," in which degenerate remains both of ovum and granulosa could be made out. The "detritus" was surrounded by a "cuticle," and the whole was contained within the vascular connective-tissue sheath ("innere Gefässschicht") or "theca folliculi." At another place (p. 33) in

the same paper an aborted egg is described as consisting of a "gallertartigen Masse," in which were seen degenerating cells and "vielleicht auch weisse Blutkörperchen." No mention is made by Stuhlmann of a growth or proliferation of follicular epithelial cells in connection with the dissolution of ova. The appearances thus described by Stuhlmann—and these are the only allusions in this paper to egg absorption—are those characteristic of the final stages in the process of degeneration.

Ruge (1887) in an elaborate memoir (1889) describes the histological changes which accompany the degeneration of intra-ovarian ova in two species of Amphibia, viz. *Salamandra maculosa* and *Siredon pisciformis*. Ruge's main results may be summarised as follows:—The death of the egg is followed by hypertrophy of the blood-vessels in the follicular investments, and by a proliferation of the cells thereof. In the second place, the degenerating egg is penetrated by elements derived from the follicular epithelium and from the blood-vessels. These cells become charged with yolk particles which are taken bodily into their protoplasm. The final products of degeneration are absorbed into the surrounding blood-vessels. A gradual reduction in size and ultimate disappearance of the egg are thereby effected.

In "spent" ovaries of the plaice and sole Cunningham (1898, pp. 117—122) found opaque granular masses which proved on examination to be degenerate ova. These bodies were at first thought to be diagnostic of the "spent" condition, but they were subsequently found also in immature ovaries. "Each consists of a mass of yolk globules of various sizes contained in a follicle; between the yolk globules are nuclei and cells, the latter not distinctly defined. The process which is taking place is evidently closely similar to that which I have described as occurring in an empty follicle. A proliferation of cells has taken place from the walls of the follicle towards the interior, the cells penetrating into the interior of the mass of yolk, and doubtless effecting its absorption. The question arises whether these cells

are derived from the follicular epithelium or from the connective tissue of the wall of the follicle, and I consider the latter alternative is correct."

The present observations on *Zoarces* leave no doubt as to the important part played by the follicular epithelium in the process of absorption of ova. There is, as Cunningham has remarked, a proliferation of cells from the walls of the follicle effecting the absorption of the egg, but it is certain that the source whence these cells are derived is not, as Cunningham supposed, the connective tissue of the follicular wall, but the follicular epithelium. It is this layer, and only this layer, which has to do with the absorption of the egg. The process is essentially different from what occurs in an empty follicle from which an egg has escaped. There is no proliferation of the follicular epithelial cells in ruptured follicles (fig. 27).

For the purpose of the present research numerous sections were cut of ovaries of a considerable number of immature and adult females of *Zoarces* caught at different times of the year. The material employed was for the most part fixed in Bles's fluid, and stained either with borax carmine or with hæmalum and eosin.

The follicular epithelium of small immature eggs such as are represented in figs. 6—10 may assume either of two well-marked forms :

(1) The follicular epithelium may consist of a layer of flat pavement epithelium, in which the deeply staining nuclei are disposed with their long axes parallel to the surface of the egg. The epithelium is bounded on the outside by a basement membrane, the *membrana propria folliculi*, and on the inside, next the egg, by a membrane with similar optical and staining properties, viz. the *zona radiata*. This is by far the more usual condition of the follicular epithelium. In a minority of cases, however, the follicular epithelium has a different aspect.

(2) The follicular epithelium is a relatively deep layer of columnar cells (fig. 16), whose inner ends are rounded and

impinge directly on the protoplasm of the egg, there being no intervening egg membrane. The nuclei of these cells are larger and more granular than in (1). They are orientated so that their long axes are perpendicular to the surface of the egg. The follicular epithelium may present both aspects in different regions of the same egg (fig. 16), so that over one segment of the egg the cells are of the flat variety, whilst over the rest of the surface they are turgid and more columnar. The two different conditions can be easily seen in the fresh ovary.

At first it was thought that the columnar condition of the follicular epithelium with its large granular nuclei might have some significance in relation to the nutrition of the normal egg. Three facts, however, are against this interpretation:—(1) The turgid condition of the follicular epithelium is only present in a small proportion of the follicles; (2) the zona radiata is absent; (3) eggs with follicular epithelium in this condition are frequently collapsed.

The nests of follicular epithelial cells represented in figs. 4 and 5 are probably instances of egg absorption at a still earlier stage. The nuclei of these cells have the aspect characteristic of those of the turgid epithelium just spoken of.

In sections of the ovary of an immature female 13 cm. long, and caught in February, the ovigerous pouches measured .5 mm. across. The majority of the pouches of this size contained normal eggs, with oil globules disposed in two zones; one around the germinal vesicle in the dense protoplasm there situated, another near the surface of the egg. No yolk spheres were present in these eggs.

A minority of the larger ovigerous pouches in the ovary under consideration contained degenerate ova. Two stages in the process of absorption, an earlier and a later, are represented in figs. 20 and 21 respectively. The transition from the one condition to the other is easily understood. The earlier condition will first be described. From the size of the pouch in this case (fig. 20) the egg, at the time of its

death, must have been about .4 mm. to .5 mm. in diameter. At this stage of its development the egg would contain very numerous oil globules but no yolk spheres. The theca folliculi is here no thicker than that which invests normal ova of the same size. Separating the theca from the follicular epithelium is, as usual, the fine homogeneous *membrana propria folliculi*. The condition of the follicular epithelium is shown in fig. 20. It is several—about six to eight—cells thick, except at one place (*gr.*), where the nuclei are on an average two deep. Here the cells are close together as in an ordinary epithelium. On either side of *g.* the epithelium passes by insensible gradations into the thicker tissue (*gr.*'), lining the rest of the egg cavity. In this cavity remains of a degenerating egg are still present (*e. i.*). In the thickened portion of the follicular epithelium (*gr.*') the cell limits cannot be distinguished, so that the tissue has the appearance of a ground mass of finely granular protoplasm in which are embedded numerous nuclei and vacuoles. The nuclei resemble those of the turgid follicular epithelium mentioned above when speaking of the degeneration of ova of a still earlier stage. The nuclei in such conditions of the follicular epithelium present a decided contrast to those of the surrounding theca folliculi. The nuclei of the follicular epithelium are larger, more granular, and have larger nucleoli.

Some of the vacuoles in the substance of the proliferated follicular epithelium are larger, more rounded, and have a sharper boundary than others. Doubtless the former represent oil globules which have been disengaged during the dissolution of the egg, and have been dissolved out in the course of preparation of the sections. Numerous oil vacuoles are still to be seen in what remains of the egg (*e. i.*). The follicular epithelium (*gr.*') is full of smaller, less sharply defined vacuoles. These probably contained the fatty degeneration products of the cytoplasm of the egg. At the place (*gr.*) where the *granulosa* is not more than two cells thick, and of a more distinctly epithelial character, a fragment of the *zona* is seen (2). The rest of the *zona* has disappeared, having

ostensibly been softened and absorbed by the action of the cells of the follicular epithelium. I could not find any very definite remains of the germinal vesicle in this egg. It would be interesting to know whether the degeneration of the cytoplasm succeeds that of the nucleus, or vice versâ. Unfortunately I cannot answer this question at present.

At the stage shown in fig. 21 the absorption of the egg by the follicular epithelium is completed. The ovigerous pouch in this case is about the same size as the last. The cavity originally occupied by the egg is entirely filled up with a sort of non-vascular adipose tissue, which is the product of the activity of the follicular epithelium. The latter has, in fact, become infiltrated with fat resulting from the decomposition of the egg. It is important to state that the *membrana propria folliculi* is still intact between the follicular epithelium and the *theca folliculi*, a circumstance which precludes the possibility of the fatty tissue being derived from the connective tissue. The existence of this membrane must also have prevented the entrance of leucocytes into the egg.

The *theca* here (fig. 21) is much thicker than it was in the earlier stage of the abortive follicle (fig. 20). It was found, on examining a number of such follicles, that a thickening of the *theca* follows the degeneration of the egg and accompanies the proliferation of the follicular epithelium. The cause of this thickening of the *theca* and proliferation of the *granulosa* is readily understood if we assume that these tissues do not cease to grow on the death of the egg, but continue active. In normal follicles the increase in volume of the egg keeps pace with the growth of the *theca* and of the follicular epithelium, with the result that these layers are more attenuated than in follicles in which the egg has stopped growing for some time. There is no special vascular development in the walls of these abortive follicles. The ovary in this particular case is in an immature condition, and both muscles and blood-vessels are but slightly developed.

Abortive follicles, similar in structure to those just described, and filled either partially or completely with the

fat-charged tissue of the follicular epithelium, according to the extent to which the process of absorption has gone, occurred in greater or less numbers in ovaries of all individuals examined, whether immature or mature. Ova of all ages and sizes undergo absorption in this way. Embedded in the tissue of the follicular epithelium in the larger follicles, which, from their size, must originally have contained a large yolked egg, are often seen masses of undigested yolk and remains of a broken zona radiata. Often there is a central mass of yolk separated by a space from the encroaching tissue of the follicular epithelium, which at this stage forms merely a thick lining to the egg cavity. In this central mass of yolk, free cells, with nuclei like those of the follicular epithelium, and probably derived from this source, can be seen attacking the yolk. Many of them consist of a vesicle containing a single fat globule. The latter occupies nearly the whole cell, the cytoplasm being reduced to a thin layer enclosing the globule. The nucleus of these cells has been pushed to one side by the development of the fat globule, and looks like a cap fitting over one end of the vesicle containing the drop. In other free cells one may find several fat droplets in various degrees of fusion to form a single globule. The mode of formation of fat drops in these cells of the follicular epithelium is, therefore, like what goes on in ordinary adipose tissue. In the larger abortive follicles, in which the zona is tolerably thick, the follicular epithelial cells have to soften and rupture this membrane in order to gain entrance to the egg (fig. 22). Cells of the follicular epithelium certainly do not pass through pores in the zona, as has been sometimes asserted. That the disintegration and solution of the egg membrane is due to the action of the follicular cells is a conclusion that seems to follow from certain observations on the degenerating eggs of *Zeus faber*. In this species there are three egg membranes, discounting the zonoid layer (fig. 34). On comparing ova of this species in various stages of degeneration it was found that the outer layers of the egg membrane were first

attacked, the thick fibrillar layer breaking up along the fibres, and at length dissolving completely, before the third or innermost showed any signs of disintegration.

Fig. 23 represents what is most probably a further stage in the absorption of the egg. I was unable, however, to find intermediate stages connecting this condition with that shown in fig. 21. In the latter figure the egg as such has disappeared, its substance having been resolved into fat drops which are contained in the cells of the proliferated follicular epithelium. In fig. 23 the ovigerous pouch is much contracted, being almost flush with the level of the general surface of the ovary. The theca is greatly thickened. The egg is represented by a mass of yellow granules, in which are nuclei of doubtful origin and many leucocytes. The granules are apparently not of a fatty nature. Had they been so they would have dissolved out in the preparation of the sections, and represented in the latter by vacuoles. They are probably lutein granules. Such masses of yellow granules were common in certain ovaries of *Zoarces*. They are always contained within contracted ovigerous pouches, and doubtless each represents an egg.

The presence of leucocytes in large numbers in association with yellow granules is important. Barfurth considers that leucocytes play only a subordinate part in the degeneration of the eggs of the trout. Ruge (1889), on the other hand, speaks of a simultaneous incursion of blood-cells and follicular epithelial cells into the degenerating egg, and he regards both kinds of elements as taking active parts in the breaking down of the egg. I do not find in *Zoarces* that the blood-cells play any part in the actual fatty degeneration of the substance of the egg. No blood-cells could be seen in the dead egg or amongst the cells of the proliferated follicular epithelium during the fatty degeneration of the egg. The follicular epithelium only is concerned in this process. Since the *membrana propria folliculi* may often be seen intact in follicles whose egg-cavity is entirely filled up with the fat-infiltrated tissue of the follicular epithelium as shown

in fig. 21, it is difficult to see how blood-cells could have gained access to the egg during its degeneration. In *Zoarces* leucocytes only come upon the scene at a late stage in the process, and then their function is probably to remove and convey into the blood or lymph channels the ultimate products of the degeneration of the egg, viz. the yellow non-adipose granules.¹

5. STRUCTURAL CHANGES IN RUPTURED FOLLICLES.

Forchhammer and Rathke were aware of the fact that the clavate villi of the pregnant ovary of *Zoarces* are not new formations, but are developed directly out of ovigerous pouches by hypertrophy of the tissues. Stuhlmann (1887) compares in detail the two structures, viz. "follikel" and "zotte" (villus), especially in regard to their vascular supply, which he carefully studied both in injected preparations and in sections.

Stuhlmann's account of the structure of a villus and his minute comparison of it with an ovigerous pouch are, however, based on a misconception, owing to his having selected for description not a typical or normal villus, i. e. an ovigerous pouch from which an egg had escaped, but one in which an egg had degenerated. That this is the case is perfectly clear from Stuhlmann's description and figures. Stuhlmann speaks of a peculiar tissue occupying the centre of the villus; he calls it the "Narbengewebe," and describes it as "eine netzartige protoplasmatische Grundmasse mit eingestrenten Kernen, in der man zahlreiche Vacuolen sieht." In regard to the development of this "Narbengewebe," Stuhlmann remarks that it may have originated in the ruptured follicle (!); "sehr wohl durch Degeneration des Follikelepithels und der angrenzenden Gewebespartien." This is clearly an error. A "protoplasmatische Grundmasse" with embedded nuclei and vacuoles is always associated with the fatty degeneration of the egg, as I

¹ See "Fat Absorption," in 'Schäfer's Physiology,' vol. i, p. 458.

have described above, but it is never formed in the ruptured follicle. Also the "Narbengewebe" in question is a product of the follicular epithelium, not of the connective tissue as Stuhlmann imagined.

In figs. 24—26 I have indicated how an ovigerous pouch from which an egg has escaped is converted into a villus. Fig. 24 is a longitudinal section of a recently ruptured pouch (August 19th). Figs. 25 and 26 are sections, longitudinal and transverse respectively, of villi from a pregnant ovary in February. In this ovary advanced "embryos," almost ready for birth, were present. The conversion of an ovigerous pouch into a "villus" is brought about as follows:—The pouch, which at the time of rupture is a pear-shaped and sessile vesicle (fig. 24), elongates to ultimately about three times its original size; it is now a long-stalked clavate structure (fig. 24). At the same time the egg cavity collapses gradually, and closes up by a doubling in and apposition of its walls—the theca folliculi. This layer becomes very thick after the rupture of the follicle, and the blood-vessels in it (arteries) and in the subepithelial stroma (veins) become greatly enlarged. The follicular epithelium undergoes no further development beyond a slight hypertrophy by simple enlargement of its cells; it ultimately degenerates into a few yellow granules. A similar hypertrophied condition of the follicular epithelial cells and nuclei was noted above as characterising certain follicles in which the egg is about to degenerate. The cause of this enlargement of the cells is probably the same in both cases; the egg being functionless, as in the one case, or gone, as in the other, the nutriment passing from the blood to the cells of the follicular epithelium is no longer rapidly absorbed as it would be if a functional egg were present, but accumulates in the cells, which accordingly become turgid. This turgidity may bring about the observed hypertrophy of these cells.

Growth, by simple hypertrophy, of the cells of the follicular epithelium is stated by Sobotta (1895) to characterise the formation of the corpus luteum in the mouse; and Marshall

(1901) confirms the observation, adding that karyokinesis of these cells may also occasionally occur. Beyond the fact of the enlargement of the follicular epithelial cells, the ruptured follicle of the Teleostei bears little resemblance at any stage of its development to the complicated structure known as the corpus luteum in mammals. Cunningham's (1897) observations on this head appear to be quite accurate. An approach to the mammalian condition is, however, not wanting in the case of the elasmobranch fishes (figs. 31, 32), as Giacomini (1896) has already shown.

My material for the study of the corpus luteum in *Spinax niger* is limited to two ovaries. These represent two distinct stages in the "adult cycle" of the organ. One ovary was that of a female in which ovulation had just occurred; the ova had just descended into the oviduct. Six corpora lutea were present in this ovary, corresponding to the number of eggs in the oviduct. The original openings of these follicles to the exterior had closed up. From a comparison of the size of these corpora lutea with that of a ripe ovum it is clear that a very considerable contraction of the follicle has taken place after rupture. The wall of the follicle which is opposite to its area of attachment to the ovary is folded inwards, doubtless by the force of the contraction. On sectioning the corpus luteum at this stage we find a considerable cavity more or less filled with a staining plasma of some sort, probably the liquor folliculi. The wall of the follicle is composed of three well-defined layers—endothelium, theca, and follicular epithelium. The endothelium is a single layer of uniform cells. The theca is a thick and very dense stratum of fibrous connective tissue. Towards the inside of this layer the cells and fibres are more loosely arranged, and venous blood-vessels with very thin walls, and of various sizes and shapes in section, are present. This layer abuts internally on the membrana propria folliculi, which in turn surrounds the follicular epithelium. The condition of the latter is very remarkable. It forms a thick lining to the cavity of the follicle, and is several cells in thick-

ness. Accordingly it presents a very different appearance indeed from the single layer of columnar cells surrounding the immature (fig. 19) and doubtless also the ripe ovum. It would seem at first glance as if a great proliferation of the follicular epithelial cells had taken place. I do not, however, think that there has been any proliferation. There were certainly no signs of karyokinesis in these cells. If we allow for the enormous contraction of the follicle which must have taken place, the thickness of the follicular epithelium becomes intelligible. As a result of the contraction there is no longer room for the follicular epithelial cells to remain spread out in a single layer over the inside of the theca, and accordingly some of the cells have been squeezed out between the others, so as to give the false appearance of a tissue several cells thick. The irregular arrangement and shape of the cells, especially towards the inside of the follicular epithelium, bears out this view.

The *membrana propria folliculi* in these preparations has a puckered appearance, no doubt due, partly at least, to contraction. At very numerous points in a cross-section of such a recently ruptured follicle the *membrana propria* is folded inwards, and strands of cells from the theca have grown into these folds, so that we have already a hint of the radial structure of the mammalian corpus luteum as described and figured by Sobotta (1895). The venous blood-vessels in the theca have not as yet commenced to grow in towards the cavity of the follicle as occurs later (fig. 31), and there is no trace of blood or blood-corpuscles in the cavity of the follicle, only a kind of plasma, probably derived from the secretion of the follicular epithelial cells.

Sections were also made of an ovary of *Spinax* in which corpora lutea in a more advanced stage of development were present. The ovary in question was that of a female towards the end of gestation. The young were almost ready for birth. Since this specimen was caught in the same month as the other one in which the ova had just descended into the oviduct, and in whose ovary the recently ruptured follicles

just described were present, the corpora lutea of the former specimen may be about one year old.

Sections of the advanced corpus luteum of *Spinax* are shown in figs. 31 and 32. The corpus luteum is much smaller than the recently ruptured follicle described above. Another obvious point of difference is that its cavity is full of blood-corpuscles. The latter are also present in great numbers in all the lymph spaces of this particular ovary. On the other hand, no blood was found in the spaces of the other ovary of *Spinax* previously spoken of.

The more advanced corpus luteum of *Spinax* (figs. 31, 32) exhibits a more decided resemblance to the mammalian corpus luteum, as described by Sobotta. His account of what takes place in the mouse may be thus briefly summarised. After bursting of the follicle, mitoses in the follicular epithelium cease, but the cells of the theca interna proliferate and grow into the layer of hypertrophied follicular epithelium in the form of radial trabeculae of connective tissue with blood-vessels. In the cavity of the ruptured follicle there is at first an effusion of blood, but this is absorbed later, and "Wanderzellen," together with connective-tissue cells, form a network which occupies the centre of the corpus luteum. This central nucleus of connective tissue is connected with that of the thecal wall by the radial trabeculae just alluded to. The arrangement of the connective tissue in transverse sections recalls the relations of the parts of a wheel, of which the axle, spokes, and rim are composed of connective tissue, and the spaces between the spokes filled with the hypertrophied follicular epithelium. Thus the obliteration of the original egg-cavity of the follicle is brought about by a complicated process, probably assisted by the actual contraction of the walls of the follicle. The characteristic epithelial portion of the corpus luteum arises by simple enlargement of the primitive follicular epithelium. The connective-tissue portion is formed by a proliferation (with karyokinesis) of the inner thecal sheath. Marshall's account (1901) of the corpus luteum in

the sheep is confirmatory, in the main, of Sobotta's observations. Marshall, however, records occasional karyokinesis of the follicular epithelial cells. He also maintains that the theca externa, as well as the theca interna, grows inwards between the epithelial cells, whereas Sobotta has stated that only the theca interna is involved in the process.

From a study of two stages in the development of the corpus luteum in *Spinax*, I can confirm Sobotta's observations in regard to the following points:—(1) Hypertrophic enlargement of the cells of the follicular epithelium; (2) ingrowth of the connective tissue of the theca at various points in a radial manner; (3) ingrowth of blood-vessels along with the connective tissue. These things are illustrated in figs. 31, 32.

The doubtful and difficult point to determine in the case of *Spinax* is this:—Whether the corpus luteum of the advanced stage, which is no doubt some months and may be a year old, represents a stage in the formation or a stage in the degeneration of the corpus luteum. Sobotta could find no evidence of degeneration in any of the corpora lutea of the mouse.

Giacomini (1896) also states, in regard to *Myliobatis bovina*, that the corpus luteum does not degenerate, but remains as a permanent structure in the ovary.

I have said that the cavity of the corpus luteum of the second or more advanced stage in *Spinax* is filled with blood-cells derived from the veins in the theca. These veins grow inwards radially with the strands of connective tissue (fig. 31). Amongst the red blood-corpuscles in the central cavity may be seen leucocytes and nuclei, some of which appear to be derived from the theca, and others from the follicular epithelium. Whether subsequently the blood in the central cavity is absorbed and a core of connective tissue formed in its place, as in the mouse, I cannot say. If so—that is to say, if the stage we are considering in *Spinax* is an early one in the formation of a corpus luteum of the

mammalian type,—then the development of this body in *Spinax* must be a very slow process indeed, taking many months for its completion, whereas the whole process in the mouse takes about three days.

I am inclined to think that the more advanced corpus luteum is undergoing degeneration. The signs of this are—(1) The disintegration of the inner cells of the follicular epithelium and the presence of free nuclei from this source in the cavity. These nuclei are obviously degenerating.

(2) The appearance of the nuclei in the theca. Some of these are degenerating; others are dividing amitotically (fig. 33). I may add that I have never seen karyokinesis in any of the cells of the corpus luteum of *Spinax*, either in the early or in the advanced stage. I am not, however, prepared to say that karyokinesis does not occur in the earlier stages, as I have not examined a sufficient number of sections.

(3) Degeneration of the fibres in the theca.

If, then, as the above observations seem to indicate, the corpus luteum we are considering has reached its maximum development and is now on its way to degenerate, it is clear that the structural changes which take place in the ruptured follicles of this Elasmobranch, while they present a distinct approach to the condition in mammals, are much less profound and complicated.

The corpus luteum of *Spinax* is likewise much simpler than that of *Myliobatis* according to the descriptions and figures Giacomini gives of the latter. The corpus luteum of *Myliobatis* is represented as a more or less solid body, in which the interpenetration of the follicular epithelium by trabeculae of connective tissue and blood-vessels has taken place on a large scale so that the corpus luteum looks like "a glandular organ full of epithelial tubes." In *Spinax*, on the other hand, the invasion of the epithelium by the connective tissue in the most advanced stage of the corpus luteum available for examination has only proceeded to a very slight extent.

I hope to go more thoroughly into these and other points connected with ovarian ova in a future paper.

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EXPLANATION OF THE FIGURES IN PLATES 15—17.

b. c. Blood-corpuseles. *b. v.* Blood-vessel. *cy.* Cytoplasm. *e. c.* Egg cavity. *e. i.* Degenerating egg. *em.* Endothelium. *ep.* Epithelium. *gr. gr.* Follicular epithelium. *g. v.* Germinal vesicle. *le.* Leucocytes. *ly.* Lymph space. *m. p. f.* Membrana propria folliculi. *p. v. l.* Zonoid layer. *st.* Stroma. *th.* Theca folliculi. *z.* Definitive egg membrane.

PLATE 15.

FIG. 1.—Zoarces. 13·2 cm. Feb. 24. Section at the surface of an ovary showing a “nest” of oogonia with interstitial cells. The compact, rounded form of the nest indicates its origin from a single mother cell. All the oogonia are equal in size and in the resting stage. Borax carmine. $\times 400$.

FIG. 2.—Zoarces. 13·2 cm. Feb. 24. A nest of oogonia with two developing ova, around which certain interstitial cells are already arranged, forming a follicular epithelium. Note that there is no general fusion of the oogonia to form a syncytium. Borax carmine. $\times 400$.

FIG. 3.—Zoarces. 15·5 cm. Sept. 18. Section of a nest with one developing ovum. Hermann's fluid and thionin. $\times 400$.

FIGS. 4, 5.—Zoarces. 13·2 cm. Feb. 24. Nests composed entirely of follicular epithelial cells and in contact with the germinal epithelium. Their derivation from the latter is indicated. There are no true ova in these nests. Borax carmine. Zeiss D, ocular 4.

FIG. 6.—Zoarces. 13·2 cm. Feb. 24. Section of young ovum showing first appearance of the “yolk-nucleus” as a brightly staining cap applied to one side of the germinal vesicle. Borax carmine. Zeiss A, ocular 4.

FIG. 7.—Zoarces. 13·2 cm. Feb. 24. Section of developing ovum, slightly larger than last. The “yolk-nucleus” has moved away from the germinal vesicle, and is now spherical with reticular structure. The “centrosphere” (?) is also shown as a dark roundish body in contact with the germinal vesicle, and looking like an extruded nucleolus. Borax carmine. Zeiss A, ocular 4.

FIG. 8.—Zoarces. 13·2 cm. Feb. 24. Still larger ovum in section. “Yolk-nucleus” seen as a circular zone of coarse fibrils in the cytoplasm. It does not stain so intensely as in the earlier stages. The “centrosphere” (?) also has moved outwards, and now lies in the “yolk-nucleus” zone. Borax carmine. Zeiss A, ocular 4.

FIG. 9.—Zoarces. Section of developing ovum showing “yolk-nucleus” around the germinal vesicle. Space between the yolk-nucleus and peripheral protoplasm. Hæmalum. Zeiss A, ocular 4.

FIG. 10.—*Zoarces*. Section of more advanced egg with "yolk-nucleus" breaking up into fragments, the more internal of which are "dissolving." Hæmalum. Zeiss A, ocular 4.

FIG. 11.—*Zoarces*. Section of ovum with yolk-nucleus cut tangentially to show reticular structure of the same. Hæmalum. Zeiss A, ocular 4.

FIG. 12.—*Zoarces*. 15.5 cm. Sept. 18. Section of more advanced ovum. The "yolk-nucleus" has broken up into fragments, and the latter are "dissolving." Amongst the fragments of the yolk-nucleus are clusters of very minute oil drops (not well shown in the figure). The centrosphere (?) in upper left-hand corner has enlarged, and is degenerating. Hermann's fluid and thionin. Zeiss A, ocular 4.

FIG. 13.—*Zoarces*. 13.2 cm. Feb. 24. Young developing ovum slightly more advanced than that shown in Fig. 6. Yolk-nucleus has severed its connection with the germinal vesicle, but is still hemispherical. Vacuoles in the yolk-nucleus are shown. Borax carmine. $\times 400$.

FIGS. 14, 15.—*Zoarces*. 80 cm. From section of the ovary. Karyokinetic division of oogonia. Hæmalum. Zeiss D, ocular 4.

FIG. 16.—*Zoarces*. Section of small ovum, showing turgid condition of the cells of the follicular epithelium over greater part of the surface, indicating commencing degeneration of the egg. Carmalum. Zeiss A, ocular 4.

FIG. 17.—*Zoarces*. Section at the surface of an immature ovum, .5 mm. in diameter, showing membrana propria folliculi, follicular epithelium, zona radiata, and (next the vitellus) the zonoid layer. Hæmalum. $\times 400$.

FIG. 18.—*Zoarces*. Section at the surface of a nearly ripe egg, 2.5 mm. Here the zona radiata is much thicker, and the zonoid layer has disappeared. Hæmalum. $\times 400$.

FIG. 19.—*Spinax niger*. Section at the surface of an immature ovum, 1.5 mm. in diameter. The follicular epithelium has withdrawn from the egg membrane, and its cells are seen to be provided with fine processes which enter into the membrane. Borax carmine. $\times 400$.

FIG. 20.—*Zoarces*. 13.2 cm. Feb. 24. Section of an abortive follicle. The follicular epithelium has proliferated, and is filling up the cavity originally occupied by an egg, remains of which are still present (*ei.*). At one place (*gr.*) the follicular epithelium still retains its epithelial character, and is only one or two cells deep. In the same region fragments of the zona radiata remain. In the dead protoplasm of the egg and in the follicular epithelium may be seen vacuoles, representing the fatty products of degeneration of the egg, and oil droplets. Borax carmine. Zeiss A, ocular 4.

PLATE 16.

FIG. 21.—*Zoarces*. 13.2 cm. Feb. 24. Portion of a transverse section of the ovary. The egg cavity of the large ovigerous pouch in the middle of the figure is entirely filled up with the tissue formed from the follicular epi-

thelium, and containing the fatty degeneration products of the egg. Borax carmine. Zeiss A, ocular 4.

FIG. 22.—Zoarces. Section of an aborted follicle, showing proliferated follicular epithelium bursting through the softened zona. Remains of the egg (*v. ei.*) are seen in the centre, invaded by free cells derived from the follicular epithelium. That part of the follicular epithelium which lies inside the zona is charged with fat. Borax carmine. $\times 90$.

FIG. 23.—Zoarces. 13.3 cm. Sept. 15. Section of an abortive follicle, showing a later stage in the absorption of the egg. The ovigerous pouch is much contracted, and scarcely projects beyond the general surface of the ovary. The theca folliculi is greatly thickened. In the centre is a mass of yellow granules, amongst which are scattered white blood-corpuscles and nuclei of doubtful origin. Carmalum. $\times 400$.

FIG. 24.—Zoarces. Semi-diagrammatic longitudinal section of an ovigerous pouch from which an egg has recently escaped. From an ovary of August 19th.

FIG. 25.—Zoarces. Longitudinal section of a "villus" from a pregnant ovary in February. On the same scale as last figure.

FIG. 26.—Zoarces. Transverse section of a "villus" in the plane of *a b* of Fig. 25. On the same scale.

FIG. 27.—Zoarces. Section of a portion of a "villus" from an ovary of October. The egg cavity is much compressed, and the follicular epithelium has not proliferated. Zeiss A, ocular 4.

PLATE 17.

FIG. 28.—*Chimæra monstrosa*. Section at the surface of an immature ovary, showing young follicle with membrana propria folliculi enclosing a follicular epithelium, consisting of small cells, also two large cells, of which the one to the left is certainly an ovum, while the smaller one to the right is probably a "nutritive" cell like those in Figs. 29, 30. Iron hæmatoxylin and orange G. $\times 400$.

FIG. 29.—*Chimæra monstrosa*. Section at the surface of an egg, about 4 mm. in diameter, nearer the animal pole, showing the many-layered follicular epithelium with differentiation of its elements; small cells on the side of the follicular membrane and large "nutritive" cells on the side of the egg. The egg membrane is here thin but dense, and clearly limited on both sides. Zonoid layer as in *Zoarces*. Streams of nutriment passing into the yolk are indicated. Iron hæmatoxylin and orange G. $\times 400$.

FIG. 30.—*Chimæra monstrosa*. Section at the surface of the same egg, but nearer the vegetable pole, showing the long-drawn-out processes of the follicular cells passing through the substance of the much modified egg membrane. The latter is much deeper than in Fig. 29, and has an open fibrous

structure, with no well-defined limit on the side of the follicular epithelium. Iron hæmatoxylin and orange G. $\times 400$.

FIG. 31.—*Spinax niger*. Part of a transverse section of a corpus luteum from the ovary of a female in which the young were almost ready for birth, showing hypertrophied follicular epithelium invaded by radial invaginations of thecal connective tissue bearing venous blood-vessels. Iron hæmatoxylin. $\times 130$.

FIG. 32.—*Spinax niger*. Portion of the same "corpus luteum" more highly magnified. Iron h. $\times 400$.

FIG. 33.—*Spinax niger*. Nuclei from the theca folliculi of the same "corpus luteum," showing stages in amitotic division. $\times 450$.

FIG. 34.—*Zeus faber*. Section at the surface of an immature egg, showing three definitive egg membranes and a zonoid layer. $\times 420$.

FIG. 35.—*Sygnathus acus*. Section of a series of small ova near the free edge of the ovigerous lamella, showing dendritic appearance of the "yolk-nucleus" around the germinal formic-formol-alcohol mixture. $\times 130$.

FIG. 36.—*Sygnathus acus*. Section of small ova near the edge of ovigerous lamella, showing the effect of Perenyi's fluid in dissolving out the "yolk-nucleus." $\times 130$.

FIG. 37.—*Zeus faber*. Section of immature ovum, showing the relation of the "yolk-nucleus" to the oil droplets. The latter are represented in the figure by minute circles.

A New Koenenia from Texas.

By

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With Plate 18.

DURING the later part of July I received from Bonham, Texas, a small package of soil containing *Koenenia*, which was sent by Miss Florence Rhine. The distance from Bonham, which is in the northern part of the State, near Red River, to Austin was so great, and the heat at that time was so intense, that the soil, which was in a paper box, became perfectly dry before it reached me. However, on placing the dry earth in a large dish of water, several specimens of *Koenenia*, in a wrinkled and distorted condition, were floated out and taken up with a brush. The wrinkles were smoothed out, by the use of KOH, to an extent that allowed of a partially satisfactory examination of the exoskeleton. The first glance at the ventral surface of an adult female revealed the fact that an entirely new species of *Koenenia* had been taken.

A hasty review of the eleven specimens obtained from the dry soil showed eight to be adult females and three immature forms. Hoping to obtain perfect specimens, I immediately wrote Miss Rhine for more material, asking that it be sent in 70 per cent. alcohol. At the same time I wrote for informa-

tion on the conditions under which the little Arachnids were found, for I thought I knew the soil of Bonham to be made up of a black-waxy alluvial, entirely free from stones. This condition would necessitate their living entirely in the soil, independent of stones—a condition which I suspected to obtain in the case of *K. wheeleri*, though the prevalence of several stones in the soil where the latter were found made it more doubtful.

In immediate reply to both of my requests, on August 3rd I received fifty-five specimens of the new *Koenenia*, and the following information in regard to their environment:—"I was looking under a cedar hedge for a suitable soil for ferns, shortly after a rain, when I discovered the *Koenenia* which I sent you. In that place the soil was moist to the depth of several inches, and there the animals were found in greater numbers than I had ever seen them in Austin. I could hardly dig up a spoonful of the soil that did not contain as many as four specimens. The top of the earth was of a dark reddish-brown colour, due to the deposits for years of decayed cedar branches; below this the soil was very dark, and here the *Koenenia* were readily observed moving about incessantly. There were no stones anywhere in the neighbourhood, the conditions being unlike those found in Austin. On receiving your letter asking for more material, I was sorry to find the earth quite dry, and no *Koenenia* in sight. In the evening, however, I watered the hedge thoroughly, and early the next morning I procured as many as I supposed you would want."

On examining the fifty-five specimens sent, I found that they consisted principally of adult females, though a few represented two developmental stages. Hoping to get individuals of both sexes, I again begged for more material, and on August 29th received fifty-six specimens, while in September sixty more were added, making in all one hundred and eighty-two specimens which I had received. Careful examination of all these revealed the same condition that was found in the case of the European *K. mirabilis*, of which

not a single male had been taken up to the present time. This seemed all the more remarkable, since in the other Texan species (*K. wheeleri*) the males at times predominate.

Koenenia florenciæ, n. sp.

In size *K. florenciæ* measures from 2 to 2·3 mm. In its proportions it is not unlike *K. wheeleri*.

Cephalothorax.—The labrum presents a laterally compressed condition, and viewed from the ventral or dorsal surface, appears to terminate in a peak. Five pairs of labral hairs are present. These hairs are as prominent as the corresponding ones in *K. mirabilis*, and twice as prominent as those of *K. wheeleri*, where they might be easily overlooked. The hypostome presents the usual cross-furrowed appearance, resulting from the arrangement of the delicate hairs of that region. The frontal sense-organ is of normal appearance, projecting forward from under the blunt-pointed carapace. The lateral sense-organs consist of three pairs of spindle-shaped hairs with the proximal ends blunted at their point of attachment. These sensory setæ are six times as long as they are broad at their broadest axis, and are dotted over with delicate hairs. They lie close to the head, and point forward and inward, arising in such a manner that when seen from above they can hardly be counted, so nearly do they lie in the same dorso-ventral plane. When seen from the side they stand out with great distinctness. The number and arrangement of the dorsal hairs of the cephalothorax are not characteristic of the species, inasmuch as the same arrangement is met with in *K. wheeleri*. There are five cross-rows of hairs; the first consisting of one pair, the second, third, and fifth, each of two pairs, and the fourth of three pairs of setæ. The number and arrangement of cephalothoracic sternal hairs are characteristic of the species. In every specimen examined for this purpose except one, which had six, five prominent setæ are present. These arise in a slightly curved line, which extends over about a third of the

breadth of the animal across the mid-ventral line. Another characteristic of *K. florenciæ*, which appears even in the delicate exoskeleton of the youngest stage, is a tongue-shaped thickening of the sternum between the fifth pair of appendages.

Chelicerae.—On the ventral surface of the proximal joint of the chelicerae three setae arise in a line parallel to the sides of the labrum. These setae present distinguishing features characteristic of the species. In *K. florenciæ* the first one of these hairs is very large,—in fact, it is the largest hair to be found on the entire body of the animal; while the other two setae are very small in proportion. The corresponding setae in *K. wheeleri* which are similarly arranged are all of the same size, blunt, and delicately plumulose near the ends. In the case of *K. mirabilis* the first of these hairs is large, but not nearly so large as the corresponding ones in *K. florenciæ*. The size and relative proportions of these setae can best be ascertained from an examination of figs. 9, 10, and 11 of the plate. The two distal joints have each eight teeth with their denticles. The teeth, in recently killed specimens, show a delicately plumulose structure, a condition which was also found in *K. wheeleri*. On the fixed blade the row of teeth ends with a sharp angle, while the moveable blade, which ended with a number of serrations in *K. wheeleri*, terminates with the last tooth. A peculiar arrangement in the fixed blade of *K. florenciæ*, which is so prominent as to make it worth mentioning, can best be made out from fig. 12 of the plate. This condition, though not so prominent, is also observed in the movable joint. It is a bulb-like attachment appearing in the cavity of the blade, on a line with the penultimate tooth. Extending from that side of the bulb nearest the teeth is a chitinous rod which becomes fused with the wall of the blade after extending down the cavity for its whole length.

Other Appendages.—The pedipalps conform throughout to the corresponding appendages in the other known species. The last leg, like that appendage in *K. wheeleri*, has, on the

upper surface of the metatarsus, a large, hollow, sensory seta, which arises at about the middle of the joint. As would be expected from our knowledge of the other members of this group, *K. florenciæ* has the usual number of seven delicate sensory setæ. The first one arises from the outer surface of the patella, one third of the distance from its distal end. The next two arise from the upper and distal limit of the first metatarsus, while the second metatarsal joint bears one on the proximal limit of its upper surface, and one near the middle on the outer surface. The fourth metatarsus and second tarsus each gives off one of these hairs from its upper surface. So far as I am aware no statement has been made in regard to the proportionate length of these delicate organs. In *K. florenciæ* the uppermost hair of the first metatarsus and the one arising from the second tarsus are only of about half the length of the other metatarsal hairs, while the corresponding hair of the patella is lacking somewhat in length. Bifurcating hairs are present on the first and second metatarsus, and second and third tarsus. Characteristic of the species is the size and the situation of the large, hollow, flat seta of the third metatarsal joint. This seta is situated at about one half of the distance from the proximal end of the joint. It is shorter and narrower than the corresponding organ in *K. wheeleri*, which arises from the distal end of the joint. In *K. florenciæ*, on the opposite side of the joint from where the seta arises, is another hollow though round and pointed seta, which is much longer and almost as broad.

The Abdomen.—In *K. florenciæ* is found the usual belt of setæ on all eleven of the segments except the first. It is in the arrangement of these setæ that *K. florenciæ* differs from all of the other described species. Along the dorsal and lateral surfaces of the abdomen, a strip, made conspicuous by the absence of setæ, extends to the seventh segment. The remaining are regularly adorned with setæ at approximately equal distances apart. The most striking differences between the two Texan *Koenenia* are to be found on the ventral surface of the abdomen. No lung-sacs are present in *K.*

florenciæ. In sections, however, the region corresponding to the lung-sac areas reacts to stains in exactly the same way as do the cells around the inverted lung-sacs of *K. wheeleri*. Specimens stained in borax carmine show three pairs of deeply stained patches on the ventral surfaces of segments 4, 5, and 6. The arrangement of the setæ on the ventral surface is entirely different from any other described species. On segments 4, 5, and 6, just over the peculiarly stained areas above mentioned, there is a crowding of the setæ of the belts, so that two groups of four setæ each are observed on each side of the mid-ventral line. From their situation these setæ correspond to the four pairs of protective setæ of the lung-sacs of *K. wheeleri*. Like *K. siamensis*, *K. florenciæ* presents an identical appearance of the ventral surface of segments 4, 5, and 6. Segment 7 is likewise lacking in a seta on its mid-ventral surface, while all the remaining segments are regularly supplied with setæ, which occur much oftener than in the other segments.

Reproductive Appendages.—Only the female appendages can be described, since males were lacking among all the specimens taken. Why such a condition exists in all the other species except *K. wheeleri* is a matter yet to be accounted for. While the males are lacking, the females must suffice to give specific character. In describing the appendages of the female almost the same description will hold good for *K. florenciæ* as was given for *K. wheeleri*. The anterior unpaired appendage of the second segment appears more pointed when viewed from below; while, when seen in profile, the sides of the appendage project backward and upward, forming a very deep trough with very thin sides. So thin are the lateral extensions of this appendage that they are easily overlooked in specimens thoroughly cleaned in KOH. The setæ of this appendage consist of ten pairs. The first row at the base, made up of three pairs, curve slightly downward. The second row of two pairs is situated further down on the appendage, and curves slightly in the opposite direction. The remaining hairs are arranged

in a somewhat irregular row on and near the edge of the appendage. The paired triangular appendages of the third segment, as usual, have three pairs of setæ—two long ones, arising on the posterior surface or from underneath, when viewed from the ventral surface, and a small one situated on the side of each appendage. The blades of these appendages are more pointed than the corresponding ones in *K. wheeleri*. Shining through the unpaired portion, and opening between the bases of the two paired ones of the reproductive appendages, is seen the large seminal vesicle, which is nearly oval in outline. This vesicle in *K. wheeleri* was flask-shaped, with the neck of the flask projecting downward. Figs. 6 and 7 of the plate show the true condition of these appendages better than any amount of description.

Flagellum.—When the material reached me through the mail the flagellum had been broken off in every case except one. This was an adult female, which had only twelve joints in the flagellum. However, I found floating around in the alcohol in which the specimens were sent, one flagellum of fifteen joints (counting the first small joint, which is never detached with the flagellum, but always remains with the body), another of fourteen joints, and another of twelve joints. In all these cases none of the proximal joints had been broken off except the small joint of which I have made mention. In these four flagella the second, third, fourth, sixth, eighth, and tenth joints had two whorls of setæ; a plumulose whorl of long setæ running around the middle of the joint, and a smooth terminal set which fitted closely over the subsequent joint. Always following the joint bearing the double whorl of setæ which precede the segment-bearing whorl of hairs are the very short, thick-walled sub-joints which may be looked upon as the anterior portion of the large joints, to which they are immovably attached. The terminal joint in two cases had two whorls of plumulose setæ; in the other two flagella it bore only one whorl. In every instance, except in the number of joints, the flagellum carries out all the observations made on the corresponding appendage in *K. wheeleri*.

Immature Stages.—These would be hardly worth mentioning, so fragmentary is the information obtained from two periods in the life-history, were it not that these two stages may give characters which phylogenetically are of the utmost importance. As is always expected in considering the young of any Arachnid, the hairs are few in number when compared with the adult, so these points can be passed over lightly except where hairs appear as specific characters of *K. florenciæ*. Of special importance, however, is the development of the reproductive appendages of the second and third abdominal segments. We saw that these appendages of *K. wheeleri*, in passing through their developmental stages, not only gave an inkling of the condition to be found in the male appendage of the adult, but also of the relative position of the species within the order. In *K. florenciæ* the older known stage presents characters in the reproductive appendage which become entirely lost in the adult female, but which resemble, in their possession of papillæ, the male appendages in *K. wheeleri*. The appendage of this stage in *K. florenciæ*, with greater elaboration brought about in its further development, probably becomes the male appendage of the adult; further collection, however, at different times of the year is needed to prove the truth of this conclusion.

Youngest known Stage.—The labrum presents the peaked condition found in the adult. One lateral sense-organ is present on each side. The number and arrangement of setæ on the carapace agree with the adult condition. Only one cephalothoracic sternal hair is present; this is situated on the mid-ventral line. No sensory hairs appear on the first metatarsus. The flat, hollow, and slightly curved seta situated on the outer side of the third metatarsus, one third of the distance from the proximal end, is present as in the adult. The characteristic setæ of the proximal joint of the chelicerae occur as in the adult. The arrangement of setæ on the ventral surface of the abdomen is very regular. Beginning with the second segment and ending with the seventh segment

there are two longitudinal rows of hairs on either side of the mid-ventral line. In segment 3 these hairs are placed farther apart and farther from the mid-ventral line, thus making the longitudinal lines slightly curved. The seventh and eighth segments have one seta on each side of the mid-ventral line, while segments 9, 10, and 11 have one on each side and one on the mid-ventral line.

Second and Last known Stage.—The labrum is compressed laterally, and has four pairs of hairs. Usually two lateral sense-organs are present on a side, though in one case only one was observed on a side. There are three cephalothoracic hairs. The appendages have all the characteristics present in the adult. On the ventral surface of the abdomen the fourth, fifth, and sixth segments have each a group of three hairs, to the right and left respectively of the mid-ventral line, while the seventh segment has only one on a side; the eighth and eleventh segments have each three setæ, one on, and one on each side of the mid-ventral line; while the ninth and tenth segments have each four setæ arranged at equal distances apart across the ventral surfaces. It is the peculiar condition of segments 2 and 3 that makes this stage of the utmost importance. These segments are prolonged into appendages that give promise of becoming male appendages, inasmuch as they possess papillæ, a condition which has been found only in the male. The second segment is prolonged posteriorly and ventrally into a trowel-shaped appendage, slightly notched at the edge, giving it a paired appearance. There projects from its edge on either side of the mid-ventral line a papilla tipped with a plumulose spine. This appendage has four pairs of setæ, two pairs forming a downward curving row, while the two remaining pairs form an irregular row near the edge. The third segment gives rise to the usual pair of projections, which are supplied on the outer side with a small seta. Figs. 13 and 14 of the plate represent camera drawings of the front and side view of these simple appendages.

The Endosternite.—Characteristic of the Arachnida is

this endoskeleton, which lies in the cephalothoracic region between the nerve chain below and the stomach above. This organ, which is easily overlooked in *K. wheeleri*, has not been described for that species, but it has already been observed in *K. mirabilis* and represented in section by Mr. Börner. In *K. florenciæ* the endosternite comes out perfectly into view while a specimen is being treated with KOH. In *K. wheeleri* this is not the case, and unless one is on the sharp look-out it entirely escapes the notice, so readily does it dissolve away on the use of KOH, along with the surrounding muscle and nervous tissue. In *K. florenciæ* the endosternite is a **V**-shaped continuous plate, slightly swollen at the sides in the region between the fifth appendages. Posterior to these swellings, and more medianly situated, are two large triangular perforations, which may be said to divide the plate into two regions, an anterior **U**-shaped portion and a posterior **V**-shaped portion, which contains the above-mentioned perforations. Near the anterior limits of the arms of the **U** are two pairs of small oval apertures, while in the outermost edge of the base of the **U** are three oval apertures on either side. The attachment of the muscles of the endosternite I did not attempt to make out. Fig. 15 of the plate will make much clearer than descriptions can the structure of the endosternite.

Systematic.—Following the discoveries made by Dr. Silvestri of two species of *Koenenia* in South America, and by Dr. Mortensen on the island of Koh Chang, in the Bay of Siam, of two other species, comes the new North American and North Texan *Koenenia*, which makes it seem all the more probable that the hitherto rare order is well represented over the globe. That one of the South American species—*K. chilensis*, Hansen—possesses lung-sacs, while the other—*K. grassi*, Silvestri—does not, and that the same condition occurs in the case of the two North American species—*K. wheeleri* possessing lung-sacs, while *K. florenciæ* does not,—is a point of great interest which invites further

consideration. From an analytical standpoint, the presence of these lung-sacs in some species only, seems sufficient ground for a definite and well-marked division of the genus *Koenenia* into two sub-genera. Mr. Börner¹ was the first to make the suggestion, basing the distinction on the condition of the reproductive appendages. Unfortunately he was misled, by Dr. Wheeler's mistaken description of the male for the female, into believing that the appendage of the second abdominal segment in *K. wheeleri* was paired, and represented a more primitive condition; hence he placed *K. wheeleri* under the sub-genus *Prokoenenia*, while the then only other known species, *K. mirabilis*, he placed under the sub-genus *Eukoenenia*. However, inasmuch as *K. mirabilis* presents a slightly paired or notched condition of the reproductive appendage, and inasmuch as *K. wheeleri* passes through a stage in its development² which is more nearly comparable to *K. mirabilis*, their position in the sub-genera would have to be reversed if we attempt to carry out Mr. Börner's suggestion. With his permission, then, I adopt his sub-genera *Prokoenenia* to include all species possessing lung-sacs, and *Eukoenenia* to include those species not possessing lung-sacs.

In regard to exact characters indicative of the species, further observations will have to be made before anything like a definite and concise analytical table can be arranged. Of the three species which I have been able to examine and compare—*K. wheeleri*, *K. mirabilis*, and *K. florenciae*—the relative size of the three more distal setæ of the proximal joint of the chelicerae was a prominent and characteristic feature of the species. In descriptions³ of the other four species no stress is laid on the distinction; and the setæ are figured in only one of the species, *K. angusta*. For the

¹ "Zur äußeren Morphologie von *Koenenia mirabilis*, Grassi," aus dem 'Zoologischen Anzeiger,' Bd. xxiv, No. 652, p. 551.

² 'Zoologische Jahrbücher,' 1903.

³ "On Six Species of *Koenenia*, with Remarks on the Order Palpigradi," H. J. Hansen, 'Entomologisk Tidskrift,' 1901.

three species which I examined, the ventral view showing the relative size of these setæ, the arrangement of the hairs of the fourth, fifth, and sixth segments of the abdomen, and the number and arrangement of the cephalothoracic sternal hairs, give an immediate clue to the species. In arranging any analytical table these specific points should come first in consideration. The females, which probably differ from the males only in their reproductive appendages, must be used entirely in furnishing the description for the species.

A. Lung-sacs present on the ventral side of the fourth, fifth, and sixth segments of the abdomen.

Prokoenenia.

1. Between the lung-sacs on segments 4 and 5 are three pairs of long backward turning hairs. These hairs are absent on segment 6. A group of four shorter hairs is present for protection over the aperture on each lung-sac. Usually fifteen cephalothoracic sternal hairs are present, eight of which are arranged in a transverse row, and seven form a V anterior to this row. The three setæ of the proximal joint of the chelicerae of equal size. Labrum rounded anteriorly, and possessing along its lip six pairs of delicate hairs. A group of four lateral sense-organs present on a side. The stiff, hollow seta is situated on the distal limit of the third metatarsus of the first leg.

Koenenia (Prokoenenia) wheeleri. Rucker.

2. No long hairs are present between the lung-sacs. Ventral surfaces of the fourth, fifth, and sixth segments are alike. A group of three hairs is present over the orifice of each lung-sac. Eight cephalothoracic sternal hairs are present, arranged at the corners of two concentric rectangles. Two lateral sense-organs are present on a side. The flat, hollow seta is situated at the middle of the third metatarsus of the first leg.

Koenenia (Prokoenenia) chilensis. Hansen.

B. Lung-sacs absent from the ventral surface of the fourth, fifth, and sixth segments of the abdomen.

Eukoenia.

3. "On the ventral surface, a group of five or six spine-like setæ on the fourth segment, and a protruding wart with six procurved setæ on the sixth segment." Two slightly curved, transverse rows of five and six setæ respectively are present on the sternum of the cephalothorax. The three setæ of the proximal joint of the chelicerae are all of different lengths, the most distal one being decidedly the longest. Labrum more rounded, with five pairs of lip hairs. One lateral sense-organ present on a side. The hollow seta of the third metatarsus of the last leg is inserted at the middle of the joint.

Koenenia (*Eukoenia*) *mirabilis*. Grassi.

4. Fourth segment of the abdomen has on its ventral side one seta on each side of the mid-ventral line, while the fifth and sixth segments have two setæ on a side. Three cephalothoracic sternal hairs are present arranged in a transverse row. A group of three lateral sense-organs are present on a side. The stiff hollow seta is inserted near the base of the third metatarsus of the first leg.

Koenenia (*Eukoenia*) *angusta*. Hansen.

5. Ventral surfaces of the fourth, fifth, and sixth segments of the abdomen have, on each side of the mid-ventral line, two setæ. Seven cephalothoracic sternal hairs are present, arranged in two intersecting diagonal rows. A group of three lateral sense-organs is present on a side. The stiff, hollow seta is inserted at the middle on the third metatarsus of the first leg.

Koenenia (*Eukoenia*) *siamensis*. Hansen.

6. Ventral surfaces of the fourth, fifth, and sixth segments have on each side of the mid-ventral line a group of four hairs. The cephalothoracic sternal hairs consist of five,

arranged in a transverse row. The anterior seta of the proximal joint of the chelicerae four times longer than either of the other two. Labrum compressed laterally to a point, and possessing on its lip five pairs of hairs. A group of three lateral sense-organs is present on a side. The flat, hollow seta situated one third of the distance from the proximal limit of the third metatarsus of the first leg.

Koenenia (*Eukoenenia*) *florenciæ*.

7. Ventral surfaces of the fourth and fifth segments of the abdomen with a group of four hairs on each side of the mid-ventral line, while only three pairs of hairs are present on the sixth segment. Eight cephalothoracic hairs are present, irregularly arranged. A group of three lateral sense-organs is present on a side. The stiff, hollow seta is inserted near the base of the third metatarsus of the first leg.

Koenenia (*Eukoenenia*) *grassii*. Silvestri.

In conclusion I have arranged in a convenient form the table given below, which records the places from which the species were taken, together with the more prominent characters of each species.

	K. mira- bilis.	K. wheel- eri.	K. chil- ensis.	K. an- gusta.	K. siam- ensis.	K. grassi.	K. floren- cia.
Lung-sacs	0	3 pairs	3 pairs	0	0	0	0
Hairs of chelicerae	1 large, 1 medium, 1 small	3 of equal size.	Undeter- mined	1 large, 2 small	Undeter- mined	Undeter- mined	1 very large, 2 small
Number of cephalothoracic sternal hairs	10 to 11	15	6	3	7	8	5
Hairs between lung-sac area .	Segment 4, 5 or 6; segment 6, 6	Segment 4, 3 pairs; segment 5, 3 pairs; segment 6, none	0	0	0	0	0
Number of hairs in group over lung-sac area of fourth seg- ment	—	4 pairs	3	1	2	4	4
Number of hairs in group over lung-sac area of fifth seg- ment	—	4	3	2	2	4	4
Number of hairs in group over lung-sac area of sixth seg- ment	—	4	3	2	2	3	4
Number of lateral sense-organs in a group	1	4	2	3	3	3	3
Type locality	Italy and Sicily	Austin, Texas	Chile	Koh Chang, Bay of Siam	Koh Chang, Bay of Siam	Paraguay	Bonham, Texas.

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EXPLANATION OF PLATE 18.

FIG. 1.—Dorsal view of *K. florenciæ* (8 oc. \times 3 obj.). The setæ of head, thorax, and abdomen are shown in their natural position. The abdomen is slightly rolled to the left, so that the broad strip along the mid-dorsal line which is devoid of setæ is not so striking.

FIG. 2.—Ventral view of the head and thorax of *K. florenciæ* (1 oc. \times 7 obj.). The arrangement and position of setæ of the proximal joint of the chelicerae are shown. The distal joints of the chelicerae which often obscure the setæ are not drawn. The characteristic peaked condition of the labrum with its curved row of five pairs of hairs is shown. The five cephalothoracic sternal hairs are shown in their natural position. The peculiar thimble-shaped thickening of the sternum between the fifth pair of appendages appears in all the stages as is figured here in the adult.

FIG. 3.—*a*. Lateral sense-organs in natural position when viewed from above. *b*. The same seen from the side and slightly displaced through pressure (8 oc. \times 7 obj.).

FIG. 4.—Frontal sense-organ (8 oc. \times 7 obj.).

FIG. 5.—The first leg of the left side beginning with the patella. The relative lengths of the sensory hairs are correctly drawn (1 oc. \times 7 obj.).

FIG. 6.—Female reproductive appendages (1 oc. \times 7 obj.).

FIG. 7.—Ventral surface of abdomen of adult female showing position of setæ (8 oc. \times 3 obj.).

FIG. 8.—*a*. Large seta from proximal joint of chelicera of *K. florenciæ*. *b*. The corresponding seta of *K. wheeleri* (8 oc. \times 7 obj.).

FIG. 9.—Chelicera of *K. florenciæ* when seen from the under side (1 oc. \times 7 obj.).

FIG. 10.—Chelicera of *K. mirabilis* when viewed from the inner side (1 oc. \times 7 obj.).

FIG. 11.—Chelicera of *K. wheeleri*. Same view and same magnification.

FIG. 12.—Tip of fixed joint of chelicera of *K. florenciæ* showing the peculiar chitinous arrangement in its cavity (8 oc. \times 7 obj.).

FIG. 13.—Side view of the reproductive appendages in the oldest ontogenetic stage found (8 oc. \times 7 obj.).

FIG. 14.—Front view of the same region which has been flattened out through pressure.

FIG. 15.—Endosternite as seen from above (8 oc. \times 7 obj.). The broad transverse piece with its lateral enlargements containing three oval apertures lies in the region between the fifth appendages.

**Oligotrema psammites: a New Ascidian
belonging to the Family Molgulidæ.**

By

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With Plates 19—23.

THE interesting little Ascidian which forms the subject of this paper was dredged by Dr. A. Willey from a depth of fifty fathoms off Lifu, New Britain, and was sent to me among a collection of Zoanthids made in the same locality. Externally the animal has so little resemblance to an Ascidian, and has so many features resembling those of Anthozoa, that it might well be mistaken for a member of the latter group. The body is sack-shaped and covered with grains of sand, like that of a Zoanthid. The mouth, or more correctly, the branchial aperture, is transversely elongated and bordered by tumid lips (Fig. 2), and there is a circlet of six pinnate arms or tentacles resembling those of an Aleyonarian surrounding the mouth. The internal organs can only be distinguished as a dark mass through the translucent walls of the body, and the atrial siphon is so small and inconspicuous that it might easily escape observation. My attention was at once attracted by the presence of six pinnate tentacles, and, suspecting that the animal was new to science, I cleared it for preliminary examination in dilute

glycerine, which rendered the test transparent and exposed clearly the intestine, the atrial aperture, and the other structures shown in Fig. 1. Further examination left no doubt that the animal was an Ascidian.

As I was unwilling to destroy the single specimen, I attempted to work out its anatomy by dissection, and with this object in view I made a longitudinal incision in the test, as shown in Fig. 3, and afterwards cut through the body just below the circumoral arms in order to study the latter structures; but the tissues proved to be so brittle and fragile after long immersion in spirit that I abandoned any further attempt at dissection, and embedded the two parts into which the animal was divided in paraffin. A series of sections was cut and stained with borax carmine, followed by picro-nigrosin or picro-indigo-carmin. Though the epithelia were in many places detached or peeled off from the underlying tissues, the general histological preservation was good, and in most cases the cell elements, even of the fragmented epithelia, were remarkably well preserved. I have therefore been able to make a tolerably exhaustive study both of the anatomy and histology of the animal, but before going into details I will define the genus and species.

Family MOLGULIDÆ.

Oligotrema, nov. gen.—Body sack-shaped; the branchial and atrial apertures distant; the branchial aperture terminal, large, transversely elongated, surrounded by a circle of six muscular, pinnate arms or tentacles. The atrial aperture minute, without lobes, placed on a small papilliform eminence of the test near the hinder end of the body on the dorsal side. The branchial sack much reduced and confined to the anterior third of the body.

Oligotrema psammites, n. sp.

With the characters of the genus. The test thin, but tough, translucent; its whole surface covered with hair-like processes, to which sand-grains are attached; these capilli-

form processes are moderately long on the outer (aboral) surfaces of the arms, short over the remainder of the anterior three-quarters of the body, long over the posterior quarter.

Length of the body (antero-posterior), 17·5 mm.; average diameter of the body, 8·75 mm.; measurement from tip to tip of the expanded arms, 10·25 mm.

Habitat—Lifu, New Britain, 50 fathoms. Only a single specimen was collected by Dr. Willey.

As I find it difficult, if not impossible, to give an intelligible account of the anatomy of *Oligotrema* while retaining the use of the term “mantle,” and as the nomenclature of the layers of which the Tunicate body is composed is in a state of confusion in this and other respects, I must, before giving a detailed account of the structure of the species, enter into a short explanation of the morphological value of the different layers, and propose some new terms which, I hope, will tend to prevent obscurity.

The different coats or layers of the Tunicate body are generally described as follows, beginning from the outside:—(1) The test (it has also been called the external tunic), which is essentially a cuticular structure, much modified by the presence of abundant intrusive mesoderm elements. Its composition and relations are well understood, and require no further mention in this place. (2) The mantle (also called the inner tunic, body-wall, etc.). This sheet of tissue, encircling the whole body, is covered on its outer surface by a layer of epithelial cells, which is the external ectoderm. Its internal surface is lined by an epithelial layer, also of ectodermal origin, the atrial epithelium; and between these two there is a mass of tissue, consisting of a form of connective tissue permeated by blood-spaces and sinuses, and containing circular and longitudinal muscle-fibres, the gonads, the renal organ, heart, stomach, intestine, etc., embedded in it. The so-called mantle is separated by a considerable space, the peribranchial or atrial chamber, from (3) the branchial sac, the wall of which is made up as follows:—Externally there is the atrial epithelium; inside

this there is a layer, for the most part thin, of connective tissue channelled by blood-spaces; within this, again, and lining the cavity of the branchial sac, is the endodermal epithelium. The walls of the branchial sac are, in most simple Ascidians, so extensively pierced by the branchial slits or stigmata that the arrangement of their component layers is not obvious, but in *Oligotrema* the branchial sac and the number of the stigmata are so much reduced that the relations are very clearly seen in sections. The arrangements just described are, of course, well understood, and have been particularly clearly explained by Yves Delage, and Herouard in the eighth volume of the 'Zoologie Concrète;' but these authors, while showing a true appreciation of the morphology of Tunicates in other respects, seem to me to make a grave mistake in describing the complex of blood-spaces in the connective-tissue layers of the "mantle" and branchial sac as a "schizocœle." A schizocœle, as defined by the authors of the name, is a form of cœlomic cavity distinguished by its mode of development from an enterocœle. The blood-sinuses in the "mantle" and branchial sac are not cœlomic spaces, but contain blood, and are appropriately classed under Professor Lankester's term hæmocœle. Moreover we know that, in some simple Ascidians at any rate, the cœlom is developed as an enterocœle from outgrowths of the primitive gut, but is obliterated early in larval life by the conversion of its walls into mesenchyme, which fills up the space not occupied by the nervous system and notochord, between the ectoderm and endoderm. The term schizocœle, therefore, is doubly unfortunate.

Equally unfortunate, I think, is the term "mantle" applied to the outer layers of the body-wall. It suggests, and was originally intended to suggest, a genetic relationship with the mantle of Mollusca, but this view has long since been abandoned, and the name has now only the sanction of long usage to recommend it. Furthermore it is misleading, for it implies an external coat formed as an outgrowth from the body-wall, whereas the so-called mantle is in fact the body-

wall, and contains most of the important viscera, as well as the musculature and the nerve-ganglion. It may most correctly be described as the external part of the body-wall, which has been, as it were, accidentally cut off from the internal part surrounding the pharynx (and in *Oligotrema* the œsophagus) by the ingrowth of the atrial and peribranchial cavities.

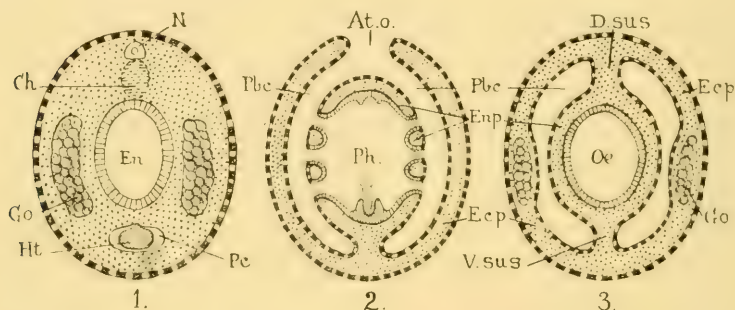
In the light of our existing knowledge of development and comparative anatomy, a Tunicate must be regarded as an animal in which the primitive cœlom has been obliterated and its place taken by a mass of connective tissue permeated by an irregular system of blood-spaces and sinuses (hæmocoel). In the adult the cavities of the gonads, and possibly the pericardial cavity¹ and the lumen of the renal organ, are the only representatives of the original cœlom. Considered from this point of view the Tunicate is a solid animal,—that is to say, the space between the gut and the external epithelium is theoretically filled up with mesodermic tissue, except for the relatively small cavities of the gonads, the pericardium, and renal organ. To this mesodermic tissue I propose to give the name *plerome*, from *πλήρωμα*, a thing filled up.²

If we imagine the formation of the atrial cavity to be delayed to a much later period of development than is actually the case, a transverse section taken midway through the body of an Ascidian, before the establishment of the atrial cavity, would have the characters shown in the annexed diagram, Fig. 1. The area shaded with dots represents the *plerome*. The atrial cavity would be formed from two dorso-lateral invaginations of the ectoderm, which would become confluent in the dorsal region and give rise to a flattened sac, overlying the dorsal aspect of the pharynx and opening

¹ The pericardial cavity of Ascidians, being formed from the ventral wall of the pharynx, may possibly be regarded as an independently developed portion of the enterocoel.

It may be objected that this term is already used by botanists. But its botanical connotation is so different from that now proposed, that it is unlikely that any inconvenience can arise.

to the exterior by the atrial aperture. The ventro-lateral horns of this sac would push their way downwards right and left of the gut to form the right and left peribranchial cavities, and in so doing would divide the plerome into an inner moiety surrounding the gut, which we may call the endoplerome, and an outer moiety forming with the external ectoderm the wall of the body. This latter moiety is what is usually called the mantle; I propose to call it the ecto-



1.—Section of a hypothetical Tunicate larva before the formation of the atrial and peribranchial cavities. The mesoderm (plerome) is a solid mass of tissue in which the gonads and the heart enclosed in its pericardium are embedded.

2.—Diagrammatic transverse section through the pharynx of an Ascidian showing the plerome divided into an outer layer (the ectoplerome) and an inner layer (the endoplerome), surrounding the pharynx.

3.—Diagram of a section through the œsophagus of *Oligotrema psammites*. *At. o.* Atrial aperture. *Ch.* Notochord. *D. sus.* Dorsal suspensory fold. *Ecp.* Ectoplerome. *Enp.* Endoplerome. *En.* Enteron. *Go.* Gonads. *Ht.* Heart. *N.* Nerve-cord. *Oe.* œsophagus. *Pbc.* Peribranchial cavities. *Pe.* Pericardium. *Ph.* Pharynx. *V. sus.* Ventral suspensory fold. The ectoderm is represented by a thick broken line; the plerome (mesoderm) is shaded with dots.

plerome. It contains the gonads, renal organ, heart, intestine, and other viscera. On the formation of the branchial slits the endoplerome of the branchial sac is, of course, broken up, and is represented by the mesoblast of the branchial bars, as indicated in the diagram in the text, Fig. 2. In most Ascidians, owing to the great size of the branchial sac, the endoplerome is practically reduced to the blood-

sinuses in the branchial meshwork; but in *Oligotrema*, in which the branchial sac is very small, and the œsophagus and stomach are relatively larger and occupy the posterior two-thirds of the body, the endoplerome is a well-defined, continuous sheet of tissue surrounding the œsophagus and anterior portion of the stomach. As the peribranchial cavities do not meet in the mid-ventral line, the branchial sac, and in *Oligotrema* also, the œsophagus and stomach, are attached to the ventral body-wall by a partition consisting of a sheet of plerome covered on both sides by atrial epithelium. This is the ventral or sub-endostylar suspensory fold. There is a similar dorsal suspensory fold separating such prolongations of the right and left peribranchial cavities as extend beyond the limits of the cloaca. The relations of these folds to the ecto- and endoplerome are shown in the diagram in the text, Fig. 3. A justification for this somewhat lengthy discussion of facts already well known will be found, I hope, in the practical utility of the terms I have proposed. I will now give a detailed description of the anatomy and histology of *Oligotrema*.

The Test.

The external appearance of the test has been mentioned in the description of the species. It is relatively thin over the greater part of the body, but is locally thickened in the neighbourhood of the branchial and atrial apertures and on the external aspects of the proximal moieties of the arms. It is involuted to a considerable extent, both at the branchial and atrial apertures. The branchial involution forming the branchial siphon is thick, and its free surface is thrown into a number of longitudinal folds. The atrial involution of the test is thin, but extends for some distance inwards (fig. 34). The substance of the test is homogeneous, or in some places shows traces of fibrillation, and gives the cellulose reaction with sulphuric acid and iodine. It contains numerous immigrant corpuscles (amœbocytes), which are nowhere swollen up to form the large vesicular cells common in the tests of simple

Ascidians. The amœbocytes of the test are generally elongate-oval in form, sometimes irregular and amœboid in shape; each contains a small, deeply staining nucleus, situated to one side of the cell; the cytoplasm is vacuolated, and in most cases contains granules of various forms. In some cases the granules are of a bright yellow colour, and these will be described more particularly further on. The hair-like processes or villi of the test do not differ from those described in many other Molgulidæ and in some Cynthiadæ. The villi are longest and most numerous on the rounded posterior (aboral) end of the body; they are almost equally abundant, but shorter and thicker, on the outer faces of the arms; they are short and more sparsely distributed over the rest of the body. The villi are hollow, and most of them contain amœbocytes; some of them, especially the longer ones at the posterior end of the body, end in enlargements, to which grains of sand are fixed, like those of *Molgula* (*Anurella*) *roscovita* figured by de Lacaze Duthiers. The villi of the arms and body, however, have bluntly pointed or rounded extremities, and sand-grains, sponge spicules, etc., are attached to their sides by a flocculent yellow material, which, as I shall show presently, is probably excreted by some of the amœbocytes of the test. The substance of the test is penetrated in all parts of the body by somewhat sparsely distributed, knobbed, and tassel-like vascular processes of the body-wall. These will be more conveniently described in connection with the ectoderm, but it may be mentioned that they do not penetrate, or, as far as I could determine, enter into any relations with the hair-like villi of the test.

The Ectoderm.

The relations of the external ectodermal epithelium to the test could not be very satisfactorily studied owing to the shrinkage of the tissues of the body-wall and their separation from the test. In some places the epithelium was adherent to the test; in others it remained adherent

to the body-wall. In both cases it could be seen to consist of a single layer of somewhat flattened, fusiform cells, whose pointed extremities interdigitate. These cells are easily recognisable because of the numerous minute granules of black pigment scattered through their cytoplasm (fig. 29, *ect*). Over the greater part of the surface of the body the ectodermal epithelium appears to be simply a flat layer applied to the internal surface of the test, but in the neighbourhood of the bases of the arms and the branchial siphon the relations between test and epithelium are more intimate. In these regions the body-wall is produced into irregular branching processes, covered with pigmented ectoderm, which penetrate into the softer and apparently semi-fluid internal layer of the test, as is shown in fig. 29. (In the figure the processes in question are separated from the test by shrinkage due to preservation in spirit.) In many of the pigmented ectoderm-cells there are yellow granules which are apparently formed in the ectoderm-cells themselves, for I could not find any traces of similar granules in the amœbocytes of the plerome in this region. But the amœbocytes which are passing through the ectoderm or have passed through it into the test are loaded with yellow granules (fig. 29, *amc*). It seems that the amœbocytes—one of them is shown clearly at *amc*—pick up the yellow granules formed by the ectoderm, and when loaded with them migrate into the test, pass through it, and discharge their contents on its free surface, thus forming the sticky, flocculent deposit which attaches grains of sand, sponge spicules, and other foreign substances to the test. Similarly amœbocytes laden with granules pass down the lumina of the hollow villous processes of the test.

The pigmented external ectoderm also enters into the composition of a peculiar form of tissue found on the ventral sides of the bases of the arms. The diagram, fig. 34, shows that near the bases of the arms there are recesses or indentations of the body-wall, and that the space between test and body-wall is prolonged some way into the body. These

recesses are, of course, lined by ectodermal epithelium, and at their inner ends the epithelium is prolonged into a number of ramified ingrowths, which penetrate deeply into the plerome in much the same manner as the allantoic villi penetrate into the trophoblast of a mammal. Fig. 25 is an enlarged drawing of the area indicated by the reference number 25 in fig. 6. It is not sufficiently magnified to show details, but it exhibits the general relations of the tissues of this region, showing the powerful muscular bands of the sphincter, the longitudinal muscle-bands, *l. mus.*, inside of these bordering on the cavity *w*, and numerous well-defined blood-spaces, *bl*. The intrusive ectodermic ingrowths, *ec. i.*, are distinguished by their numerous dark nuclei, and the drawing gives a good idea of their number and extent, and of the relations they bear to the other tissues. Fig. 30 is a highly magnified drawing of a portion of fig. 25, showing the ectodermal ingrowths, *ec. i.*, formed of the characteristic pigmented ectoderm-cells, many of which contain yellow granules. The ingrowths penetrate into the blood-spaces, and there can be little doubt that the whole structure is subservient to the nutrition of the test.

The two tubes marked *vp*. in the same figure, whose walls are composed of one or more layers of cells with deeply stained nuclei, are cross-sections of two of the tassel-like vascular processes described above as penetrating the substance of the test in all parts of the body.

The general appearance of these vascular processes is best shown in fig. 5, *vp*. They are most abundant on the arms, but occur over the whole surface of the body, and, as the body-wall has shrunk away from the test, some of them have been pulled out of the crypts into which they fitted and remain adherent to the body-wall; others have been torn away, and remain embedded in the test. They vary very much in length; those on the arms are quite short, as shown in fig. 5, but in other parts of the body they may be of considerable length, penetrating for a long way into the substance of the test. Each is a simple tubular outgrowth containing a cavity,

which on the one hand communicates with the blood-spaces of the plerome, on the other hand ends blindly at the knobbed distal extremity of the process. The single or double layer of epithelial cells composing their walls is continuous with the external ectoderm, but differs from the latter in not containing pigment granules. I was at first inclined to regard these processes as sense organs, but as I have been unable to find any nerve-fibres in connection with them or to distinguish any sense-cells on them, I must conclude that they are simply vascular processes, serving partly to attach the body-wall to the test, partly to aid in the nutrition of the latter.

The characteristic pigmented ectodermal epithelium also forms a lining to certain remarkable cavities which lie right and left of the branchial sphincter muscle. The relations of these cavities, which may possibly be artefacts due to contraction in spirit, will be described further on.

The atrial epithelium differs considerably from the external ectoderm, consisting of a pavement epithelium composed of very much flattened polygonal cells, devoid of pigment granules, and fitting closely to one another by their edges. The transition from the pigmented external epithelium, involuted along with the test into the atrial siphon, to the unpigmented atrial epithelium is abrupt. In the neighbourhood of the anus the atrial epithelium is modified. There is a tract of columnar, flagellated cells leading from the anus to the atrial siphon. These cells are very similar in shape to the curious flagellated cells forming the lining epithelium of the branchial sac, which will be described in connection with that organ.

The Plerome.

As described above, the body of *Oligotrema* must be thought of as if there had been a solid mass of tissue (the plerome) between the external ectoderm and the gut. Into this mass the atrial cavity has insinuated itself and, spreading right and left of the gut and branchial sac, has divided the plerome into an outer layer, the ectoplerome, corresponding

to the "mantle" of previous authors, and an inner layer, the endoplerome, surrounding the gut. The inner surface of the ectoplerome and the outer surface of the endoplerome are, of course, covered by atrial epithelium. As the atrial cavity does not extend to the extremities of the body, there is posteriorly a solid mass of undivided plerome in which part of the stomach and testis are embedded, and anteriorly the plerome is undivided and is produced into six muscular processes which are the six circumoral arms.

The bulk of both the ecto- and endoplerome, as well as the anterior and posterior undivided portions of the plerome, is made up of a form of connective tissue consisting of a structureless or sometimes slightly fibrillated matrix in which a few corpuscles are embedded. This matrix stains, like all intercellular substance, with picro-nigrosin and picro-indigo-carmin, and its characters are fairly well shown in figs. 22, 26 and 30. The connective-tissue matrix is honey-combed with irregular cavities, and the muscles and all the principal organs of the body are, as it were, embedded in it. The blood-spaces have no regular arrangement, and I could not find any trace of definite blood-vessels such as occur in most simple Ascidians, unless a delicate pavement epithelium lining some of the larger cavities near the heart might be taken as an indication of regular blood-channels.

Musculature.

All the muscles of the animal are contained in the ectoplerome or in the undivided plerome of the anterior end. There is no trace of a layer of muscle-fibres surrounding the gut or the branchial sac. The general arrangement of the muscles is shown in figs. 3 and 4. The musculature is weak, except in the regions of the atrial and branchial siphons and the arms. Over the greater part of the body it consists of a series of thin longitudinal bands, placed rather far apart, and these are crossed at right angles by a series of circular bands, the two series forming a rectangular

network with rather open meshes. The arrangement of these muscle-bands in *Oligotrema* is exceptional in that the circular bands are external and the longitudinal bands internal.

Towards the posterior end of the body the musculature diminishes and eventually dies out altogether, but it is strongly developed round the atrial siphon. The last-named structure is a long, narrow tube formed by the walls of the ectoplerome, and in a surface view, such as is shown in fig. 3, it might easily be taken for a continuation of the intestine. The muscles in this siphonal tube are arranged, like those of the body-wall, as an external layer of circular and an internal layer of longitudinal muscle-bands, which here are relatively very numerous and form a rectangular network, with very fine meshes.

Immediately below the branchial aperture the circular muscle-bands are gathered together to form a strong sphincter surrounding the mouth. This branchial sphincter (fig. 4, *sph.*) lies above a ring of thickened tissue surrounding the mouth, and embraces the branchial siphon. It is chiefly made up of a number of flat, concentric, muscular bands, which extend outwards over the bases of the tentacular arms in such a manner as to give a hexagonal figure to the sphincter. These circular muscle-bands are to be regarded as the constrictors of the branchial orifice, and they are crossed by a number of much finer radial bands or dilators of the branchial orifice, whose inner ends are inserted on the thickened ring of tissue mentioned above. The same ring of tissue serves for the attachment of the longitudinal muscles of the body-wall and the flexor muscles of the arms, to be described further on. The muscle-bands of the dilators, as well as those of the constrictors, branch, and the branches of the latter inosculate with one another in a complicated manner, especially at the bases of the arms (fig. 5, *sph.*). At the base of each arm a bundle of muscle-fibres is given off from the outermost band of the sphincter and branches freely in the substance of the arm, the branches looping round in the manner shown in fig. 5, and uniting again to form a number

of bands which run back down the length of the arm and are inserted, like the dilators of the branchial orifice, on the ring of thickened tissue surrounding the mouth. One of these longitudinal bands, situated on the internal or adoral aspect of the arm, is especially large and thick (fig. 5, *mus. flex.*) and is to be regarded as the flexor muscle of the arm, bending it inwards towards the branchial orifice; while the slips derived from the outermost band of the sphincter would appear to act as extensors of the arm, lying as they do on its outer or aboral aspect. One may infer, from the arrangement of the muscles, that the arms in the living animal could be closed rapidly and powerfully over the branchial orifice, and would therefore be serviceable in capturing prey; but it should be noticed that the lateral offsets of the muscular core of each arm, which obviously fit into the pinnæ, contain no muscular slips. It must be concluded, therefore, that while the arm as a whole is movable, the pinnæ are incapable of independent movement.

The presence of muscular arms surrounding the branchial opening, though not unknown, is an unusual feature in Tunicata. The only Tunicate having arms comparable in size and complexity to those of *Oligotrema* is *Octacnemus*, and there is some resemblance in the arrangement of the muscles in these two forms. But the anatomy of *Octacnemus* differs so much in other respects from that of *Oligotrema* that there can be no question of close relationship, and one must look for a nearer homology to the six denticulate muscular lobes surrounding the branchial aperture of *Ctenicella*, which in turn are modifications of the six simple lobes characteristic of the branchial aperture of the *Molgulidæ*. Other *Ascidians*, of course, have similar lobes, but the number is not the same. The circumoral lobes of *Ctenicella* are described by de Lacaze Duthiers as muscular, and as having each one terminal and two pairs of lateral pinnæ. If they were largely increased in size, and their lateral pinnæ were multiplied and complicated by branching, and the circlet of lobes were somewhat further removed from the branchial

aperture, the lobes of *Ctenicella* would bear a strong resemblance to the arms of *Oligotrema*. In the former genus the atrial aperture is also surrounded by denticulate lobes, four in number. These are not present in *Oligotrema*, but their absence is easily accounted for by the reduction of the atrial siphon. In my specimen the muscular branched lobes, a single one of which is shown in fig. 5, were so much shrunk by the action of spirit that they fitted loosely into the corresponding cavities of the test (fig. 4); but there can be no doubt that in life they fitted close into these cavities, and that each arm, though covered by a tough coat of test, was capable of a considerable amount of movement. It should be observed that the muscles are not continued into the lateral processes which must have fitted into the pinnae, and it would therefore appear that while the arm could move as a whole, the pinnae were incapable of independent movement. Every muscle-band is made up of a number of fairly long tapering muscle-fibres, each with a nucleus situated at about the middle of its length. The individual fibres exhibit a faint longitudinal striation and are crescentic in cross-section, the nucleus lying in the concavity of the crescent (fig. 29, *mus.*). I was unable to find any trace of undifferentiated protoplasm surrounding the nucleus.

The Atrium and Peribranchial Cavities.

The relations of the atrium and peribranchial cavities are best seen in the series of sections, figs. 8—15, and are also indicated in the diagram fig. 34, which is a reconstruction of my series of sections. The lumen of the atrial siphon is narrow (fig. 15, *at. si.*); internally it opens into the wide atrium or cloaca, *at.*, which lies, like a flattened sac, over the dorsal surface of the stomach, and extends right and left over about one third of its lateral surfaces. As explained above, the test is invaginated for a considerable distance at the atrial aperture, and forms a thin but perfectly distinct lining to the narrow atrial siphon, extending as far as the openings of

the oviducts and the anus. Posteriorly the atrium is prolonged backwards on the right side of the body as far as the lowest limit of the bend of the intestine, but there is no corresponding cavity on the left side. Anteriorly the atrium extends forward between the stomach and the dorsal body-wall (ectoplerome) to about the middle of the length of the body, and is there interrupted by the dorsal suspensory fold (fig. 34, *D. sus.*); but laterally it extends right and left of the stomach and œsophagus towards the mid-ventral line, to form the right and left peribranchial cavities (fig. 13, *R. pbr.* and *L. pbr.*), separated from one another by the ventral suspensory fold. The peribranchial cavities are prolonged forward far beyond the limits of the atrium itself; as shown in fig. 12, they are completely separated from one another (except for their communication by way of the atrium) before they reach the level of the branchial sac. In the region of the branchial sac the peribranchial cavities continually diminish in size as they pass forwards (figs. 8 to 11), until in the most anterior branchial region they are reduced to mere canals, which lie dorsally right and left of the branchial sac, and eventually end blindly in front. The left peribranchial cavity is deeper dorso-ventrally, and extends rather further forward than the right. The limits of the right peribranchial cavity are indicated by the deeper shade of blue in fig. 34.

The walls of the atrium and peribranchial cavities, where they are not bulged by the gonads, intestine, and other viscera embedded in the ectoplerome, are for the most part smooth and devoid of ridges and folds. But in the œsophageal region a thick, longitudinal ridge of the ectoplerome, covered, of course, by atrial epithelium, projects into the peribranchial cavity of either side. As these ridges are highly vascular—that is to say, they contain an exceptional number of blood-spaces crowded with corpuscles,—they are probably respiratory in function, and I regard them as the representatives of the endocarps of other Ascidians.

The Branchial Siphon, Branchial Sac, and Gut.

The general relations of these organs and of the other viscera associated with them are shown in figs. 3 and 34, and in the series of sections, figs. 6 to 15. The branchial aperture has the form of a transversely elongated slit, and the branchial siphon, lined by a thick involution of the test, is also compressed in the transverse plane. The mouth at the bottom of the branchial siphon is not a circular orifice, but is narrow and slit-like, and slants dorso-ventrally owing to the branchial siphon being produced backwards on the ventral side to form a sort of half tube or gutter, crescentic in section. The mouth is surrounded by a circle of small, ramified, oral tentacles. I was unable to determine the number of these tentacles from my sections, but they are fairly numerous. I should judge that there are sixteen or more, and they are distinctly, but not largely, ramified. They are covered by a peculiar, modified, flagellate epithelium, which also lines the prebranchial zone and a large part of the branchial sac, and will be described in detail further on.

The branchial sac is one of the most remarkable features of *Oligotrema*, both because of its small size and because of the great reduction of the characteristic structures associated with it, such as the endostyle. The latter structure, indeed, is so feebly developed that no trace of it could be seen through the transparent walls of the body, even after the specimen had been stained with borax carmine and cleared in xylol preparatory to being embedded in paraffin. Under the same conditions the branchial sac itself could hardly be recognised, but it could be discovered, on close observation, as a dilatation of the anterior end of the œsophagus (fig. 3, *Br. s.*). Its extent and relations to the branchial siphon and adjacent organs are clearly shown in fig. 34. The œsophagus is a relatively wide tube running back on the dorsal side; its length is about one third of the whole length of the body, and it is therefore a much more important and conspicuous

section of the alimentary canal than is the case in other simple Ascidians. Posteriorly its diameter gradually increases, and it passes without any obvious line of demarcation into the stomach. The stomach is flexed ventrally and has the form of a wide, U-shaped sac, occupying the posterior end of the body. The intestine takes its origin from the anterior end of the distal or ventral limb of the stomach. On leaving the stomach it passes into the ectoplerome of the left side of the body and runs backwards and towards the dorsal side; on reaching the dorsal side of the proximal limb of the stomach it turns forward and runs parallel with the œsophagus towards the atrial siphon. The anus is situated on a conical eminence in the atrium, opposite the atrial siphon. There is no trace of a digestive gland or liver, but the distal limb of the stomach is closely invested by the ramifications of the testis.

These organs may now be described in detail.

The Branchial Sac.—This organ is extremely small as compared with that of other Ascidians, its length being less than one fifth of the whole length of the body. Its relations are best understood by following a series of sections forward from the region of the œsophagus. As is shown in figs. 3 and 34, the œsophagus is a relatively long and wide tube lying on the dorsal side. Fig. 12 is a transverse section taken a short way below the posterior limit of the branchial sac. The œsophagus, invested by the endoplerome, is seen on the dorsal side attached by the thick and short dorsal suspensory fold to the body-wall. The ventral suspensory fold is long and thin, and separates the right and left peribranchial cavities from one another. Fig. 11 is a section through the extreme posterior limit of the branchial sac, and shows that here the ventral suspensory fold has become much thicker; and its ventral moiety is channelled by a few irregular passages which communicate with the right peribranchial cavity by elongated slit-like apertures or stigmata. A few sections further forward similar passages are found communicating by stigmata with the left peribranchial

cavity, and still further forward the ventral suspensory fold is conspicuously thicker and contains a considerable central cavity, into which a number of irregular lateral chambers open. These in turn communicate by slit-shaped stigmata with the right and left peribranchial cavities. Fig. 10 is a drawing of a section taken still further forward, and shows that the cavity in the ventral suspensory fold—which cavity we may recognise henceforth as the branchial sac—has increased greatly in extent and communicates by a narrow passage with the œsophagus. The right peribranchial cavity retains its size, but the left cavity is notably diminished owing to the dorsal extension of the left corner of the branchial sac. Fig. 9 represents a section taken through the middle of the branchial sac. It shows that the ventral part of the branchial sac extends widely to the right and left, and that there is a corresponding reduction of the two peribranchial cavities. The cavity of the branchial sac communicates on each side by wider or narrower orifices with a number of secondary cavities, which may be called exhalent chambers. These open in turn by numerous stigmatic slits into the right and left peribranchial cavities. The œsophagus communicates freely with the branchial sac, but is still distinct from it, and, as will be shown directly, is lined by a different kind of epithelium.

Fig. 8 is a section through the upper end of the branchial sac. The peribranchial cavities are reduced to small dimensions; the cavity of the branchial sac has increased very much in size, and the œsophagus is reduced to a deep groove on its dorsal surface; but the epithelium lining the groove is still sharply marked off by its histological characters from that of the branchial sac proper.

Still further forward, at the extreme anterior end of the branchial sac, the peribranchial cavities are reduced to mere canals, into which a few stigmata open. The groove lined by œsophageal epithelium may be traced as far forward as the prebranchial zone, and there it dies out altogether.

It should be observed that the anterior extensions of the

peribranchial cavities are pushed further and further towards the dorsal surface, so that the stigmata, which in the posterior part of the branchial sac were confined to its ventral and ventro-lateral aspects, are in the anterior part confined to its dorso-lateral aspects; and the branchial sac itself becomes progressively wider in its dorsal and narrower in its ventral moiety as one proceeds forwards. A little below the level of the branchial sphincter the ventral wall of the branchial sac is continued into the spout-shaped ventral prolongation of the branchial siphon, but the relations are somewhat complicated by the fact that in the mid-ventral line the branchial sac is produced into a short, forwardly directed diverticulum, lying ventrad of the branchial siphon. The walls of this diverticulum are thrown into longitudinal folds and are surrounded by the strong muscular fibres of the sphincter and the radial muscles taking their origin from the ring of thickened tissue round the mouth.

The result of these arrangements is that the obliquely directed mouth-opening faces the opening of the œsophagus into the branchial sac, and the stigmata are confined to a narrow zone running obliquely across from the ventral to the dorsal side of the branchial sac, nearly parallel to the mouth. These relations are clearly shown in the diagram, fig. 34. The space between the stigmata and the mouth is the pre-branchial zone.

The branchial sac is too short and the stigmata are too closely crowded near its ventral surface to leave much room for an endostyle. Reference has already been made to the fact that in the entire animal, notwithstanding the transparency of its tissues, no endostyle could be seen; nevertheless one is present, though in a very reduced and rudimentary condition.

I had great difficulty in making out the relations of the endostyle, peribranchial grooves, etc., because the epithelial lining of the branchial sac was largely peeled off and lay in strips and patches in its cavity. In places, however, the epithelium remained adherent to the walls, and even in the

detached strips the cell elements were so well preserved that I could study their details with some considerable degree of accuracy.

The œsophagus is lined by a glandular epithelium, the characters of which are shown in fig. 17. It is made up of columnar cells, with flattened nuclei situated at the extreme basal ends of the cells. The cytoplasm is filled with minute, highly refracting, yellowish granules, probably zymogen granules of some kind. This epithelium is continued up the groove on the dorsal side of the branchial sac, and may be traced nearly as far forward as the dorsal tubercle, beyond the point where the groove ceases to be recognisable.

De Lacaze Duthiers describes a groove which runs forward from the œsophageal opening alongside of the dorsal lamina in *Molgula*, with which the much larger œsophageal groove of *Oligotrema* is doubtless homologous; but I could find no trace of a definite dorsal lamina.

The epithelium lining the branchial sac and the pre-branchial zone and covering the oral tentacles is of an entirely different character to that of the œsophageal groove, being composed of elongated cells such as are figured in fig. 18, *a*, *b*, *c*. They are extremely like the collar-cells of sponges, but as I was unable, after long examination, to satisfy myself that their long projecting free ends are, in fact, hollow cylinders with a flagellum passing down the middle of each, I will simply call them modified flagellate cells. These cells, as seen in section, are hammer-shaped; the head of the hammer is basal, and the nucleus is situated where the handle is fixed on the head. Adjoining cells are fitted together by their hammer-headed basal ends, and their handles project as long, free processes into the branchial or pre-branchial cavities. The body of the cell (i. e. the head of the hammer) is more granular than the process, and stains with carmine; the process is stained, but not deeply, by picro-nigrosin or picro-indigo-carmin. In some places the free processes are short (fig. 18, *c*); in others they are inordinately long (fig. 18, *b*). In a considerable number of the cells I

was able to detect a single delicate flagellum projecting from the free extremity of each; these flagella were most often recognisable in cells from the epithelium of the tentacles. In the majority of cells, however, no flagellum could be detected, and in many cases, especially in those cells in which they were longest, the free processes are club-shaped, having rounded extremities attached to the body of the cell by a relatively narrow pedicle. This feature suggests that the cells, like the endoderm-cells of *Hydra*, may withdraw their flagella and become amœboid. Fig. 18, *b*, is a careful camera drawing of some of the best preserved of these cells, very highly magnified. The resemblance to a collar-cell is certainly very striking, especially in the tallest cell on the right hand of the figure; but it would be rash to make any positive assertion about it. It must be remembered that my single specimen of *Oligotrema* was preserved in the tropics far from a laboratory, and that it had been in spirit for a long time before it reached me. It was therefore very unlikely that the details of such delicate structures as collar-cells could be faithfully preserved, and it says much for Dr. Willey's skill and care in preserving his collections that the specimen reached me in such good histological condition as it is. Though I have looked through sections of various Ascidians belonging to the genera *Molgula*, *Ascidia*, *Phallusia*, *Ciona*, and *Styelopsis*, I have been unable to find any trace of an epithelium comparable with that of the branchial sac of *Oligotrema*, and, so far as I can ascertain, no such epithelium has been described in any other Ascidian. The nearest approach to it that I can find is a band of elongated claviform cells, described by R. Hertwig as occurring in the ventral groove (*Bauchrinne*) of *Cynthia canopus*. In some places, where they are not well preserved, the cells of *Oligotrema* resemble those figured by him; but his drawings show the nuclei near the free ends of the cells, whereas in *Oligotrema* they are situated at the basal ends.

This modified epithelium clothes the tentacles and lines nearly the whole of the branchial sac, but does not occur in

the œsophageal groove. There are also tracts in the branchial sac where it passes into a layer of simple non-flagellated cubical cells, and these in turn are succeeded by a tract of wedge-shaped, ciliated cells, as shown in fig. 18, c. A short band of these ciliated cells could be traced on the ventral side of the branchial sac, just in front of the branchial slits, and I regard this band as the representative of the endostyle. I cannot be certain of its extent, as the epithelium is largely peeled off in this region and lies in strips in the branchia sac. A similar band of ciliated epithelium can be traced on either side of the branchial sac, apparently nearly coinciding with the anterior limits of the right and left peribranchial cavities; but the condition of the epithelium prevents my saying anything certain on this point. At all events, the lateral bands of ciliated epithelium exist and run from the ventral towards the dorsal surface on either side of the branchial sac. They must therefore be regarded as representing the peribranchial grooves.

At the lips of the œsophageal groove, where the epithelium is marked with a black line in figs. 9 and 10, there is on either side a band of richly ciliated epithelium, which runs all along the lips of the groove and passes rather suddenly on their ventral side into the characteristic flagellated epithelium of the branchial sac. These bands of ciliated epithelium are very fairly well preserved; their component cells are represented in fig. 20, and it is obvious that they differ from the ciliated cells of the endostyle and peribranchial grooves, and belong rather to the category of the œsophageal epithelium. Dorsally these ciliated bands are succeeded by a tract of non-glandular cubical cells, which pass into the glandular epithelium of the œsophageal groove. These ciliated tracts may possibly represent the dorsal lamina. Their function is clearly to direct food into the œsophagus.

The Branchial Slits.—The branchial sac, as has been described, commences posteriorly as an irregular space in the thickness of the ventral suspensory fold. The thick lateral walls of the sac are honeycombed by a number of irregular

canals and chambers, which recall, more than anything else, the incurrent and excurrent canals of a sponge. The chambers open on the one hand by wider or narrower orifices into the cavity of the branchial sac, and on the other hand they communicate by means of numerous stigmata with the peribranchial cavities. The arrangement of the chambers and stigmata is so complicated that it is difficult either to figure or describe it, but some idea of their relations may be gained by a study of fig. 16, which represents the portion of the branchial wall marked *z* in fig. 9, as seen from the inner or branchial surface. The drawing is made from a model reconstructed from about thirty serial sections, and shows the lower moieties of the two incurrent branchial chambers separated by a stout vertical fold of the branchial wall; this fold probably corresponding to one of the folds in the branchial sac of *Molgula*, while the incurrent chamber is a highly modified form of a cavity of a fold. Each chamber is subdivided in a most complicated way by cross-partitions and trabeculae into a number of secondary chambers (fig. 26, *ic.*²), which are prolonged upwards and downwards far beyond the limits of the openings into the primary incurrent chambers. Both primary and secondary incurrent chambers open by numerous elongate stigmata—some of which are clearly shown in fig. 16—into the peribranchial cavity, the walls of which are in places so deeply infolded as almost to form a set of excurrent chambers into which the stigmata open. Some idea of the complexity of these folds and chambers may be gathered from fig. 26, which is a drawing of one of the sections included in the middle of the model. The stigmata are fairly numerous and for the most part irregularly arranged, but they tend to rise one above another in a scalariform manner, as shown on the left hand of fig. 16. There is no trace of a spiral arrangement. The right-hand incurrent chamber of the model has ten stigmata opening from it, and the sections above and below the limits of the model show that about as many more open into the peribranchial cavity from its anterior and posterior prolongations.

The edges of the stigmata are clothed with a ciliated epithelium so similar to that of other Ascidians as to require no description.

The Œsophagus and Stomach.

The walls of both the Œsophagus and stomach are longitudinally folded, but as the epithelium is more or less detached from the walls of the gut it is difficult to say how far the folds shown in figs. 12, 13, and 14 are natural, and how far they are due to contraction in spirit. The corresponding folds of the endoplerome in the stomach (fig. 14) indicate that in this region, at any rate, they are natural. The anterior section of the Œsophagus is lined by a glandular epithelium exactly similar to that of the Œsophageal groove; towards its posterior end the glandular cells increase in size and their nuclei become more rounded, and they gradually pass, without any definite line of demarcation, into the much longer and larger epithelial cells of the stomach, shown in fig. 27. The epithelium of the stomach is composed of very large wedge-shaped cells, with narrower basal and broader outer ends. The nucleus is situated near the basal end of each cell, is spherical, and has a distinct nucleolus. The cytoplasm of the narrower basal end is dense and finely granular, that of the broad outer end (i.e. the end turned towards the lumen of the gut) is vacuolated, and in most cases contains accretions of yellowish crystals, which are apparently products of digestion; but as I was unable to apply any micro-chemical tests to my sections I cannot say whether they are nitrogenous or not.

The form and relative size and extent of stomach and Œsophagus are clearly shown in the diagram, fig. 34. The stomach exhibits a sharp ventral flexure, and is therefore U-shaped; the walls of the distal limb are not longitudinally folded, but are lined by the same kind of epithelium as those of the proximal limb.

The Œsophagus of my specimen was empty, but both limbs

of the stomach were full of material, including an entire Crustacean, which occupied nearly the whole of the cavity of the proximal limb. As the contents of the stomach serve to throw light on the habits of the animal, I examined them carefully and found that the smaller stuff and débris in the distal limb consisted chiefly of the fragments of Crustacea of different kinds; I could recognise fragments of the limbs and mouth parts and portions of the bodies of Copepods, some of which must have been of large size relatively to the specimen of *Oligotrema* in which they occurred. The entire Crustacean in the proximal limb proved to be an Amphipod which had evidently been only recently swallowed, for it is in a good state of preservation, the head and some of the anterior thoracic somites being the only regions in which signs of partial digestion are evident. As this Amphipod was cut into numerous sections I could not even determine its genus with any certainty, but from what I could make out of the shape of its antennæ, mouth parts, and thoracic limbs, from its dome-shaped thoracic segments, its long, backwardly directed and pointed thoracic pleura, and the shape of the abdomen, the terminal segments of which are fused together, and from the large size of the eyes (which, however, had suffered partial digestion), I shall not be far wrong in identifying it as a member of the *Platyscelidæ*, and very probably it is *Platyscelus* (*Eutyphus*) *armatus*, Claus, or a closely allied species.

Platyscelus armatus was taken by the "Challenger" in surface collections made between New Guinea and Japan, and *P. rissoinæ* was obtained by the same expedition at a depth of 240 fathoms off Tongatabu. It is not unlikely, then, that this Amphipod belongs to a genus of which members have been found swimming on the surface or at considerable depths in the Pacific. At all events there is no question here of a parasitic or commensal Crustacean, such as are found in the branchial sacs of so many Ascidians. The fragments of Copepods found in the stomach are obviously the digested remains of free-living species; the Amphipod belongs in all

probability to the genus *Platyscelus*, the members of which are free living. Therefore the contents of the stomach go to prove that *Oligotrema* is able to capture and swallow relatively large and active Crustacea, a feat which its six muscular arms are well adapted to perform.

The intestine is a narrow tube which takes its origin from the left side of the anterior and dorsal angle of the distal limb of the stomach. It passes at once into the ectoplerome of the left side and runs backward, on the inner side of the ovary, towards the dorsal surface. On reaching the dorsal surface just in front of the posterior limit of the stomach it turns forward, and, still enclosed in a thickening of the ectoplerome, it is continued forward to the atrial siphon, and opens by a minute anal orifice in close proximity to it. The intestine of my specimen is empty. In the first part of its course it is lined by a glandular epithelium composed of small cells having the character, as far as their state of preservation allowed me to determine it, of somewhat squat goblet-cells. In the last section of the intestine the glandular cells give place to a columnar epithelium which appears to have an excretory function, as the free ends of its component cells are loaded with highly refracting nodules of a brownish-yellow colour (fig. 31), and a number of similar concretions are contained in the lumen. The blood-spaces surrounding this terminal section of the intestine are full of corpuscles of various kinds, whose accumulation in this region may be held to afford additional evidence of the excretory nature of the epithelium.

The Reproductive Organs.

Oligotrema, like other *Ascidians*, is monœcious. The ovaries are paired, and open into the atrial cavity near and somewhat in front of the anus, by right and left oviducts. The ovaries, as shown in figs. 3, 34, 13, 14, have the form of a pair of sinuous bands embedded in the ectoplerome of either side of the body at about the level of the atrial siphon. They

are full of ova in all stages of maturation. The riper ova are relatively large, are full of large yolk-granules, and are enclosed in follicles and furnished with reserve cells after the manner common in Ascidians. The dorsal ends of the two ovaries are continued into short oviducts, which run in the ectoplerome and open into the atrial cavity at the ends of two papilliform prominences situated a short distance in front of the anus opposite the entrance of the atrial siphon (*R. od.*, *L. od.*, figs. 34, 14, 21). The terminal sections of the oviducts are lined by a ciliated cubical epithelium.

The testes are a mass of ramified tubules closely applied to ventral and ventro-lateral surfaces of the distal limb of the stomach. There is no external indication of their being paired, nor can any sign of paired structure be discovered in sections of these organs; but the sperm-ducts are paired and open at the ends of rather conspicuous nipple-shaped prominences into the right and left peribranchial cavities close to the angle of flexure of the stomach. Fig. 22 is a representation of the left spermiducal opening with an adjacent lobe of the testis, and incidentally illustrates the structure of the gastric and intestinal epithelium and of the connective tissue of the ectoplerome. In the testicular tubules one can distinguish externally a peripheral mass of larger rounded or polygonal cells with conspicuous and deeply stained nuclei; these I take to be spermatogonia; within these a layer of smaller cells, which seem to be spermatocytes, and in the centre a mass of developing spermatids, and in some of the tubules bundles of filiform spermatozoa. The cellular elements are minute, and the organ was too much macerated to admit of detailed study.

The Blood-vascular System.

I found traces of the heart in the form of a thin-walled, muscular tube, lying in the angle between the posterior end of the renal organ and the lobes of the testis; its position is indicated at *Ht.* in fig. 34. The muscular tube is

surrounded by a distinct thin-walled sac, the pericardium, but as my sections of this region were broken by grains of sand carried through the preparation from the stomach on the edge of the razor, I was unable to make out the relations of the heart clearly, and could not determine the connection between the heart and neighbouring blood-spaces. Definite blood-channels can hardly be said to exist. The substance of the plerome is honeycombed by numerous cavities containing corpuscles, and in the neighbourhood of the heart a very delicate pavement epithelium could be detected forming a lining to some of the larger spaces. In each tentacular arm, however, there is a definite axial blood-space, which is enlarged and forms a conspicuous cavity at the base of the arm (fig. 6, *bl.*)

As a rule the corpuscles contained in the blood-spaces are few in number, but in some places they are very numerous, e. g. in the tissues at the bases of the arms, in the neighbourhood of the anus, in some of the endopleromic cavities bordering on the gut, and in the two longitudinal ridges which I have identified as endocarps. These blood-corpuscles may more appropriately be called amœbocytes. There appear to be two kinds—

1. A vesicular variety which are either (*a*) empty, when they have the form of nearly spherical vesicles (fig. 32, *c, d*) with a coarsely reticulated cytoplasm and a nucleus situated on one side of the cell; or (*b*) with cell contents, generally of a brown colour, which are sometimes arranged like a shell round the periphery of the cell (fig. 32, *e*), or are simply an aggregate of discrete granules (fig. 28, *am. c.*).

2. Granular basophile cells, such as those depicted in figs. 32, *a* and *b*, containing numerous granules which stain intensely with picro-nigrosin or picro-indigo-carmin. The granules can often be shown to be connected by fine threads, as is shown in fig. 32, *a*.

There can be little doubt that both kinds of cells are nutritive in function. As the vesicular cells are abundant in the blood-spaces surrounding the stomach, and their brown

contents are of the same colour as the crystalline concretions which occur in such abundance in the epithelium of the stomach, I regard them as nutritive cells or trophocytes. The basophile cells are possibly reserve cells or thesocytes, but as I was unable to apply micro-chemical tests to my single series of sections I could not determine the nature of their contents.

The Renal Organ.

This organ is of very large size in *Oligotrema*, and lies embedded in the ectoplerome on the right and ventral side of the gut in the position shown in figs. 34, 14, and 15. It is somewhat ovoid in shape, with a broader anterior and a narrower and tapering posterior end. Briefly described, it is a closed, thin-walled sac, lined by a peculiar epithelium, and its cavity is filled with a mass of formless coagulum, the superficial layers of which are stratified and give rise to numerous spherical, concentrically striated concretions. There are no ducts and no communications of any kind between the cavity of the organ and the adjacent blood-spaces, but the anterior two-thirds of the sac bulge into the right peribranchial cavity, and are separated from the latter by so thin a wall that the contents might easily escape by diffusion into the peribranchial cavity, and so by the atrium to the exterior. A closed renal sac of this kind, filled with concretions, is universal in the family *Molgulidæ*, and has been described by de Lacaze Duthiers and Kupffer; and a similar organ has been described by Van Beneden, Krohn, and others in various species of *Ascidia* and *Phallusia*. In *Oligotrema* the renal sac is exceptionally large, and is lined by an epithelium different from those described by the above-mentioned authors. A portion of this epithelium is represented in fig. 23. It consists of a layer of dark and finely alveolar protoplasm, in which rather large, rounded nuclei are embedded at intervals; there is no trace of cell outlines. This epithelium had been peeled off from the greater part of the inner surface of the renal sac, and the fragments were

much shredded ; it was only here and there that I was able to find adherent patches such as that represented in the figure. The strips lying loose in the cavity are very numerous, and those cut through in any section would go several times round the cavity if placed end to end—a fact which suggests considerable complication in the way of folds. The spherical concretions are often found embedded in the epithelium, as shown in fig. 24.

De Lacaze Duthiers, Kupffer, and Krohn made a careful study of the contents of the renal sacs of the species they had under observation, and agree in stating that the spherical concretions gave the murexide reaction with nitric acid and ammonia ; but in each case the reaction appears to have been faint, and their descriptions are not very convincing as to the presence of uric acid. In order to test this point I dismounted one of my slides and applied the murexide test, without obtaining any trace of a red or purple colour. The concretions and the surface layers of the coagulum were stained yellow, which suggested the xanthoproteic reaction and would seem to indicate the presence of proteid reserve material. It is obviously impossible to draw conclusions from chemical tests applied to sections which had previously undergone prolonged treatment for staining and mounting, but it is worth recording the fact that I failed to obtain the murexide reaction, for the structure and relations of this so-called renal sac are more suggestive of storage of reserve material than of an excretory organ, and the chemical composition of the concentrically striated spherules requires further investigation. In the spherules of *Oligotrema* the darker concentric bands were stained orange-red by borax carmine, and were deeply stained by hæmatoxylin. The central coagulum was unaffected by these dyes, but stained vividly with eosin ; the outer stratified layers stained in the same manner as the spherules. Fig. 33 shows the manner in which the spherules seem to be formed from the external stratified layers of the coagulum contained in the renal sac.

The Nervous System.

The nerve-ganglion of *Oligotrema* occupies the position typical in Ascidians. It was not sufficiently well preserved to admit of thorough histological examination, but there is an external layer of rather large multipolar nerve-ganglion cells surrounding a central plexus of nerve-fibres. Anteriorly three stout nerves are given off from the ganglion, one of which passes straight forward to supply the dorsal part of the sphincter and the dorsal arms. The two other nerves pass right and left of the branchial siphon and supply the lateral and ventral parts of the sphincter and the lateral and ventral arms. Posteriorly a single nerve can be traced backwards for some distance in the mid-ventral line, and smaller branches appear to be distributed to the œsophagus.

The Subneural Gland and Duct.

The subneural gland itself was not well preserved. It appears to consist of a few short tubules closely applied to the nerve-ganglion. The interior of the tubules is occupied by numerous small cells with deeply stained nuclei, but the histology of the gland could not be satisfactorily determined. The duct, on the other hand, is large, and the tall, columnar, ciliated cells forming its epithelium were admirably preserved. The duct is short, and opens by a gaping slit-shaped orifice in the mid-dorsal line of the prebranchial zone. The orifice is situated on a small eminence, the dorsal tubercle, and, as far as could be determined from the sections, it is a simple longitudinal slit; there is no evidence of the spiral twisting of its lips so commonly found in other Ascidians.

In conclusion I must call attention to the cavities marked *x* in figs. 7 and 8. The cavity in fig. 8 is a posterior diverticulum of the larger cavity shown in fig. 7, and this is seen in the latter figure to be continuous with the space formed by contraction of the tissues between the spout-shaped ventral continuation of the branchial siphon and the body-

wall. As the branchial siphon is an invagination of the test, the ectoderm is of course invaginated along with it, and as the siphon has shrunk away from the body-wall, the ectodermal epithelium remains adherent to the latter and forms a lining to it in the space just mentioned. This same ectodermic epithelium, characterised by the presence of black pigment granules, forms a complete lining to the cavity marked *x* and to its posterior diverticulum. It may further be seen that the cavity and the diverticulum are bounded by numerous strong, longitudinal muscle-bands, which, as seen in cross-section, appear to project into the cavities. The cavity with its diverticulum, shown in figs. 7 and 8, is on the left side; there is a similar cavity on the right side, with a much shorter diverticulum, but as the sections are oblique it does not appear in the figures. The ring of apparently thickened tissue lying below the branchial sphincter shown in fig. 4 is the external indication of the right cavity, and its walls are clearly corrugated by the contracted muscle-bands which traverse them. I am in doubt as to the nature of these cavities. They may, of course, be artefacts formed by deep infoldings of the ectoderm of the branchial siphon consequent upon the post-mortem contraction of the muscle-bands. But I am not inclined to interpret them as such, because of their symmetrical position right and left of the lower end of the branchial siphon and the upper part of the branchial sac. Nor can I imagine that any artificial folds due to post-mortem contractions could give rise to so well defined a diverticulum reaching so far back alongside of the branchial sac as that shown in fig. 8. Furthermore the connective tissue of the plerome adjacent to the cavities is differentiated, being far more compact and containing more numerous cellular elements than elsewhere, so as to give the appearance of a supporting structure related to the insertions of the longitudinal muscles. As it is impossible for me to form a satisfactory conclusion as to the nature of these cavities from the examination of a single series of sections, I must leave it an open question whether they are artefacts or not; but I am disposed to think

that they are in some manner connected with the insertions of the muscle-bands both of the branchial sphincter and the longitudinal muscles of the body-wall, and that their thickened walls afford support to the tissues of this region.

It is clear from the foregoing description that *Oligotrema*, aberrant as it is in many structural features, must be classed in the family *Molgulidæ*, for the following reasons :

1. The arenaceous covering to the test and hollow, hair-like, villous processes of the latter, serving for the attachment of sand-grains, though found in some *Cynthiadæ* and other *Ascidians*, are features which on the whole are characteristic of the *Molgulidæ*.

2. The six branchial arms must be regarded as the highly differentiated representatives of six branchial lobes. The *Molgulidæ* are characterised by the possession of six branchial lobes, and in the genus *Ctenicella*, a member of this family, the lobes are produced into short, muscular, tentacle-like processes provided with terminal and lateral pinnae comparable to the arms of *Oligotrema*, though very much less developed. The *Molgulidæ* are further characterised by the presence of four lobes surrounding the atrial siphon, and in *Ctenicella* these are modified in the same manner as the branchial lobes. There are no atrial lobes in *Oligotrema*, but their absence is clearly attributable to the great reduction of the atrial aperture.

3. The oral tentacles are compound, as is the case in all *Molgulidæ*.

4. The branchial sac is longitudinally folded, and the representatives of the longitudinal bars are not papillated.

5. The stigmata, though not arranged in spirals, are slightly curved. The stigmata of *Oligotrema*, indeed, do not show any marked resemblance to those of typical members of the family, but it must be remembered that the spiral arrangement does occur in all *Molgulidæ*.

6. The intestine is on the left side of the stomach, and throughout its course is embedded in the ectoplerome; or, to use the terminology of previous authors, it is attached to the

inner surface of the left side of the mantle, and is sunk in the mantle—a feature characteristic of Molgulidæ.

7. The renal organ is largely developed, is situated on the right side of the gut, and has the structure characteristic of the Molgulidæ.

8. The oviducts and sperm-ducts are paired, a feature which, though not universal in the Molgulidæ, is found in a great many members of the family.

But in classing *Oligotrema* in so well known and typical a family of simple Ascidians, its many peculiar features must not be lost sight of. These are—the wide separation of the branchial and atrial orifices; the great reduction in size of the atrial siphon and the concomitant suppression of the atrial lobes; the highly differentiated pinnate muscular arms; the great reduction in the size and extent of the branchial sac; the suppression of the dorsal lamina and the feeble development of the endostyle and peribranchial grooves; the relatively great length and diameter of the œsophagus, and the presence of a large œsophageal groove extending nearly to the anterior end of the dorsal side of the branchial sac.

It may be safely inferred, from what we know of the contents of the stomach of this single specimen, that these remarkable modifications of structure are due to changed habits of life, and particularly to a change from the mode of nutrition characteristic of other Ascidians. The large Amphipod contained in the stomach, whether I am right in referring it to the genus *Platyscelus* or not, clearly belongs to a free-living species, and is neither commensal nor parasitic. It is too large, and must have been too active, to have been swept into the mouth by the action of ciliary currents; and the same may be said of the relatively large Copepoda, of which abundant fragments are contained in the stomach. On the other hand, the size and position of the six tentacular arms, and the powerful and complex musculature with which they are provided, are satisfactory evidence of their efficiency as organs for capturing prey. *Oligotrema psammites*, then, is an Ascidian which captures and feeds on active

Crustacea of large size relatively to itself, and is no longer dependent on minute organisms and organic débris swept into its branchial chamber by ciliary currents and there filtered off from the water by an extensive branchial apparatus. Hence we find that the branchial sac, being no longer of prime importance for the nutrition of the animal, has undergone great reduction in size, as also have all those accessory organs whose function it is to secrete strings of mucus for the entanglement of the solid matter brought in by the branchial current and to direct the food by ciliary action along definite tracks to the œsophageal opening, viz. the endostyle, the peribranchial grooves, and the dorsal lamina. In consequence of the reduction in size of the branchial sac, and therefore of the stigmatic area, a relatively small current of water can pass through its meshes into the atrial cavity, and the reduction in size of the atrial siphon follows almost as a matter of course. On the other hand, the œsophagus and stomach are relatively far better developed than is the case in other simple Ascidians, and the dorsal œsophageal groove, facing the oblique elongated mouth-opening, becomes a prominent feature, being clearly adapted to transmit the organisms swallowed as food directly into the œsophagus.

In conclusion I must express my thanks to Professor W. A. Herdman, who was kind enough to read through my rough manuscript and to make many valuable suggestions, which I have incorporated in this paper; also to Professor Weldon, who, while I was working in his laboratory, assisted me from time to time in the solution of difficult problems of structure and histology. Most of all, my thanks are due to Dr. A. Willey, who, inadvertently perhaps, sent me the specimen of *Oligotrema*, which has been a subject of much interest to me.

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EXPLANATION OF PLATES 19—23,

Illustrating Dr. G. C. Bourne's paper on "Oligotrema psammites, a new Ascidian belonging to the family Molgulidæ."

LETTERING IN ALL THE FIGURES.

amc. Amœbocytes. *an.* Anus. *arm.* Tentacular arm. *arm'*. Muscular core of tentacular arms. *At.* Atrium. *At. o.* Atrial aperture. *At. si.* Atrial siphon. *bl.* Blood-space. *Br.* Branchial aperture. *Br. s.* Branchial sac. *Br. si.* Branchial siphon. *d. sus.* Dorsal suspensory fold. *dt.* Dorsal tubercle. *ecp.* Ectoplerome. *enp.* Endoplerome. *ect.* Ectoderm. *ect. i.* Ectodermic ingrowth. *ex. c.* Excurrent chamber. *gl.* Subneural gland. *gr.* Yellow granules in ectoderm. *ht.* Heart. *ic.* Incurrent chamber. *int.* Intestine. *l. mus.* Longitudinal muscles. *L. od.* Left oviduct. *L. pbc.* Left peribranchial cavity. *L. spd.* Left sperm-duct. *M.* Mouth. *mus.* Muscle-bands. *mus. dil.* Dilator muscle of branchial siphon. *mus. ext.* Extensor muscles of arm. *mus. flex.* Flexor muscle of arm. *N.* Nerve-ganglion. *n.* Nerve. *Oe.* Œsophagus. *æ. g.* Œsophageal groove. *Ov.* Ovary. *Od.* Oviduct. *pin.* Pinnæ of arms. *pl.* Plerome. *pbr.* Cavity of prebranchial zone. *R.* Renal organ. *R. od.* Right oviduct. *R. pbc.* Right peribranchial cavity. *R. spd.* Right sperm-duct. *Sph.* Sphincter muscle. *St.* Stomach. *St'.* Distal limb of stomach. *s. s.* Stigmata. *T.* Test. *tn.* Oral tentacles. *Tl.* Testis. *vp.* Vascular processes. *v. sus.* Ventral suspensory fold. *x.* Cavity (? artificial) lined by ectoderm. *y.* Bristle passed into the R. peribranchial cavity in fig. 34.

PLATE 19.

FIG. 1.—An enlarged drawing of *O. psammites* seen from the left side. The actual size of the animal is indicated by the line on the left of the figure.

FIG. 2.—An enlarged drawing of the oral aspect of *O. psammites*, showing the transversely elongated branchial aperture surrounded by six pinnate arms.

FIG. 3.—A view of the principal organs in situ, as seen through the transparent body-wall, after the test has been opened by a longitudinal cut.

FIG. 4.—A view of the branchial sphincter muscle and the six tentacular arms from below.

FIG. 5.—One of the muscular arms removed from the test, showing the arrangement of the muscles.

FIG. 6.—A section (somewhat oblique) through the branchial siphon and the bases of three of the tentacular arms.

PLATE 20.

FIG. 7.—A section through the mouth.

FIG. 8.—A section through the upper part of the branchial sac.

FIG. 9.—A section through the middle of the branchial sac.

FIG. 10.—A section through the lower end of the branchial sac.

FIG. 11.—A section through the upper end of the œsophagus, showing the thickening of the ventral suspensory fold, in which there are four small cavities, two of them opening by stigmata into the right peribranchial cavity.

FIG. 12.—A section through the middle of the œsophagus.

FIG. 13.—A section through the lower end of the œsophagus.

FIG. 14.—A section through the upper end of the stomach, showing the origin of the intestine from the ventral limb of the stomach and the openings of the oviducts.

FIG. 15.—A section passing through the atrial siphon and anus.

PLATE 21.

FIG. 16.—The inner surface of a portion of the wall of the branchial sac, showing the longitudinal branchial folds, the openings of two incurrent branchial chambers, and the stigmata opening into the latter. This drawing is made from a model reconstructed from a series of sections.

FIG. 17.—Cells from the glandular epithelium of the œsophagus.

FIG. 18—

a. Flagellate epithelium from the oral tentacles.

b.—Flagellate cells resembling collar-cells from the epithelium of the branchial sac.

c.—A portion of the epithelium of the branchial sac, showing the transition from the elongated flagellate cells to the ciliated epithelium of the endostyle.

FIG. 19.—Transitional epithelium from the œsophageal groove.

FIG. 20.—Ciliated cells from the lips of the œsophageal groove.

FIG. 21.—An enlarged drawing of the openings of the oviducts into the atrium.

FIG. 22.—Part of a section through the upper region of the stomach, highly magnified, showing the opening of the right sperm-duct.

FIG. 23.—A portion of the epithelium lining the cavity of the renal sac, highly magnified.

FIG. 24.—Two concentrically striated spherules from the renal sac, embedded in the renal epithelium (Zeiss $\frac{1}{2}$ hom. imm. comp., oc. 8).

FIG. 24*a*.—A double concentric spherule from the renal sac.

FIG. 25.—A magnified drawing of the area indicated by the reference number 25 in Fig. 6, showing the intrusive ectodermic tissue (*ec. i.*).

PLATE 22.

FIG. 26.—Part of a section through the walls of the branchial sac, highly magnified, showing the incurrent and excurrent branchial chambers and the stigmata. The drawing is made from one of the sections included in the model represented in Fig. 16.

FIG. 27.—Glandular cells from the epithelium of the stomach (Zeiss $\frac{1}{12}$ hom. imm. comp., oc. 4).

FIG. 28.—The opening of the duct of the subneural gland, highly magnified, showing the ciliated epithelium of the duct.

FIG. 29.—Outgrowths of the body-wall into the test, showing the pigmented ectodermic epithelium cells, many of which contain yellow granules (highly magnified).

FIG. 30.—A portion of the section represented in Fig. 25, very highly magnified, showing the intrusive ectodermal ingrowths (*ec. i.*) at the bases of the arms, and two vascular processes (*v. p.*).

FIG. 31.—A portion of the epithelium from the terminal part of the intestine, showing the excretory concretions.

FIG. 32.—*a* and *b*, basophile amœbocytes from the blood-spaces, highly magnified (Zeiss $\frac{1}{12}$ hom. imm., oc. 8); *c* and *d*, empty vesicular amœbocytes from the blood-spaces; *e*, a vesicular amœbocyte (trophocyte) with contents.

FIG. 33.—A portion of the stratified external layer of the contents of the renal sac, showing the formation of the concentrically striated spherules.

PLATE 23.

FIG. 34.—A diagram illustrating the anatomy of *Oligotrema psammites*. The tissues of the body-wall (ecto- and endopleurone) are represented in a light shade of blue, the gut in yellow, the test in pink, the ovaries in green, the renal organ and testis in different shades of red. The extent of the atrium and right peribranchial cavity is indicated by a darker shade of blue. The animal is represented as dissected from the right side, the right wall of the branchial sac being removed.

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CONTENTS OF No. 187.—New Series.

MEMOIRS:

	PAGE
On the Anatomy and Development of <i>Distomum cirrigerum</i> , v. Baer. By ERNEST WARREN, D.Sc., Assistant Professor of Zoology, University College, London. (With Plates [✓] 24— [✓] 26)	273
Studies in the Retina. Part VI.—The Continuity of the Nerves through the Vertebrate Retina. By H. M. BERNARD, M.A. Cantab. (From the Zoological Laboratories of the Royal College of Science.) (With Plates [✓] 27— [✓] 29)	303
The Bionomics of <i>Convoluta roscoffensis</i> , with Special Reference to its Green Cells. By F. W. GAMBLE, D.Sc., Owens College, Manchester; and FREDERICK KEEBLE, M.A., University College, Reading. (With Plates [✓] 30 and [✓] 31)	363
<i>Trypanosoma</i> in Birds in India. By W. HANNA, M.B., D.P.H., Liverpool. (With Plate [✓] 32)	433
On the Modification of the Eye Peduncles in Crabs of the Genus <i>Cymonomus</i> . By E. RAY LANKESTER, M.A., LL.D., F.R.S., Director of the Natural History Departments of the British Museum. (With Plates [✓] 33 and [✓] 34)	439

On the Anatomy and Development of
Distomum cirrigerum, v. Baer.

By

Ernest Warren, D.Sc.,

Assistant Professor of Zoology, University College, London.

With Plates 24—26.

Material.—In November, 1901, my attention was drawn by a student dissecting a male crayfish (*Astacus fluvialis*) to the condition of its muscles. The extensor muscles behind the heart contained numerous rounded bodies of a whitish translucent aspect, which varied in size from microscopic dimensions to 1.5 mm. or more in diameter. On examination these bodies proved to be cysts enclosing the trematode *Distomum cirrigerum*, v. Baer. The living animal could be seen revolving inside the cyst.

Some of the extensor muscles were stripped off and fixed in strong Flemming solution for about fifteen hours. The remainder of the crayfish was placed in a large volume of corrosive sublimate and 2 per cent. acetic acid for half an hour.

Adult forms and developing young were both found in the crayfish; the former occurred almost entirely in the extensor muscles, while the latter were chiefly embedded in the thin sheets of connective tissue over the muscles and around the nerve-cord and the endophragmal skeleton of the thoracic

blood-sinus, also in the superficial substance of the testis itself.

A remarkable circumstance in connection with fixation should be noticed here. Encysted animals, whether adult or developing, when fixed in corrosive and acetic, generally contained a large quantity of gas between the cyst-wall and the body of the animal, and it was accordingly impossible to properly embed them in paraffin until the gas had been expelled by pricking the cyst in several places. Specimens fixed in Flemming's solution did not exhibit the same difficulty; it would seem that this reagent acts in such a manner on the cyst-wall that it remains permeable to the gas, while corrosive sublimate renders it impermeable. Whether the gas is normally formed by the parasite, and in the natural state it slowly diffuses through the cyst-wall, or whether the reagents themselves acting on the body or cyst-wall produce the gas, I am unable to state. It may be mentioned in this connection that I have frequently observed the presence of large bubbles of gas in the arteries of the crayfish. A. Willey has observed a similar phenomenon in the blood-vessels of the pearly nautilus.

The crayfish was of Continental origin, and probably it came from Germany; it was my sole source of material for the present paper. I have been unable to find another infested animal, although since the investigation was commenced I have examined at least a hundred specimens.

LIFE-HISTORY OF THE SPECIES.

The life-history of *D. cirrigerum*, v. Baer, is very obscure. The animal was first observed encapsuled in the muscles of the crayfish by v. Baer¹ in 1827. Twenty years earlier, in 1808, Rudolphi² found the trematode *D. isostomum*, Rud.,

¹ Baer, K. E. von, "Beiträge zur Kenntniss der niederen Thiere" ('Nov. Act. Acad. Caes. Leop. Carol.,' tom. xiii), 1827.

² Rudolphi, C. A., "Entozoorum sive vermium intestinalum historia naturalis," vols. i and ii, Amstelod., 1808-9.

lying free among the muscles of the crayfish. This animal possesses no trace of generative organs. In 1880-81 C. O. Harz¹ ascribed the disastrous epidemic² among the crayfish of the Continent as being due to the presence of *D. cirrigerum* and *D. isostomum*. In the same year the view of Harz was proved to be unfounded by G. Zaddach,³ who published without figures short descriptions of the anatomy of the two trematodes, which are frequently found together in the same crayfish. Zaddach regarded *D. isostomum* as being a sexless phase in the life-history of *D. cirrigerum*. He propounded the following hypothesis. The cercaria swimming in the water penetrate the skin of the crayfish, become encapsuled in the muscles, and grow into the sexually mature *D. cirrigerum*. The encapsuled animals after self-fertilisation produce a heap of brown eggs and die. The eggs become scattered among the muscles of the host, and develop into the sexless unattached trematode *D. isostomum*. The crayfish containing the parasites is now supposed to be eaten by some vertebrate (pike, eel, otter, etc.), in whose intestine the trematode becomes sexually mature. Eggs are laid and pass out of the vertebrate host. Zaddach imagines that the earlier stages of the embryo are passed in a snail or some other invertebrate in the typical manner.

The evidence in favour of such a view is not very convincing, and it would render the life-history of the species highly remarkable in that there would be two sexual phases, one in the crayfish and one in some vertebrate.

Without further observations on the occurrence of *D.*

¹ Harz, C. O., "Eine Distomatosis des Flusskrebseß," 'Deutsche Zeitschr. für Thiermed. u. vergl. Pathologie,' Bd. vii, 1881; also 'Oesterr-ungar Fischerei-Zeitung' für 1880-81.

² This epidemic is actually caused by the myxosporidian *Thelohania contejeani*, Henneguy.

³ Zaddach, G., "Über die im Flusskrebse vorkommenden *Distomum cirrigerum*, v. B., und *D. isostomum*, Rud.," 'Zool. Anzeiger,' 1881. E. Gaffron describes carefully the nervous system of *D. isostomum*, 'Zoolog. Beiträge,' hrsg. von Anton Schneider, Bd. i, Breslau, 1884.

isostomum it is not possible to prove that it enters into the life-history of *D. cirrigerum*. In the particular crayfish under consideration *D. isostomum* did not occur with any absolute certainty, and according to Zaddach's theory the eggs of *D. cirrigerum* should develop into the sexless *D. isostomum*; but I have traced the development of the sexual form direct from the egg in the crayfish host. Hence we are led to one of two conclusions: either the eggs of *D. cirrigerum* in the crayfish may develop direct into the sexual *D. cirrigerum* or into the sexless *D. isostomum*, according to the season and the particular physiological condition of the host and parasite at the time in question; or *D. isostomum* has no connection with *D. cirrigerum*, and the development of the latter might be compared with that of *Aspidogaster conchicola*, which inhabits the pericardium or Keber's organ of Anodonta and other Lamelli-branchs.

Braun¹ suggests that possibly the occurrence of the sexual form in the crayfish is of the nature of an accident, and that its typical and normal host is some vertebrate.

Assuming that *D. cirrigerum* and *isostomum* are phases in the life-history of the same species, it is probable that the stimulus arising from change of host is necessary for the production of sexual organs in *D. isostomum*, and the only modification which is introduced into Zaddach's hypothesis is the probability that the eggs of *D. cirrigerum* in the crayfish may according to circumstances develop into either the sexual form which can complete its development in the same host, or into a sexless form which must be transferred to some other host before becoming sexual.

If such be the life-history of the species it is unique among trematodes; but the problem requires re-investigation in the natural surroundings of the crayfish, and my own material can throw no further light on the subject.

¹ Bronn's 'Thierreichs: Vermes, Trematodes,' Bd. iv, p. 870.

GENERAL ANATOMY OF THE SEXUAL FORM *D. CIRRIGERUM*.

The Non-Encysted Animal.—The majority of the animals were encysted in the muscles, but some few were quite free, lying among the organs of the body. I am unable to state for certain whether these were naturally free, for it is quite possible that exposure to the water after the student had opened the crayfish induced some of the animals to break out of their cyst. One individual was fixed in the act of escaping (Fig. IV).

Some of the free animals were quite small, and were far from being sexually mature, although fundaments of genital organs could be seen; while others were of full size, and had ripe eggs in the uterus. Free individuals sexually mature varied in length from about 1 mm. to about 1.75 mm., and in breadth from .50 to .75 mm. The anterior and posterior suckers are approximately equal in size, and are of very considerable dimensions, having a diameter nearly half the breadth of the body. Behind the posterior sucker the body is cylindrical, while in front it is laterally compressed, and tapers somewhat towards the anterior sucker. The genital depression lies immediately in front of the posterior sucker, and through it the cirrus is evaginated, while on the posterior border of the depression is the crescentic opening of the vagina. Terminally the excretory pore is visible, and on the dorsal surface, a little posterior to the middle of the body, is the extremely small opening of Laurer's canal, which is not visible in the whole specimen (Figs. I, II, III).

The general surface of the body is roughened by small cuticular scales, which are variable in their amount of development in different individuals. They tend to be but slightly developed in the middle region of the body, but are more conspicuous at the two ends, especially the posterior end. The scales are conical or plate-like elevations of the general cuticle; separate spinelets embedded in the cuticle, as described in some Distomids, could not be distinguished in the adult, but in the developing animal they are quite obvious

(Figs. XII, XV). Commonly the scales of the adult are about $3\ \mu$ in height. The cuticle is thickest over the hinder region of the body, and consists of two layers,—an inner vacuolated portion, and an outer, more homogeneous layer. The scales may be perfectly solid and continuous with the outer homogeneous layer (Fig. XVI), or they may be vacuolated and appear like bubbles¹ on the surface of the cuticle (Fig. XVII). The cuticle and scales were very inconspicuous in the free young individuals.

The general body parenchyma beneath the cuticle is of the usual type. The so-called epidermal cells (Fig. XVI, *ep. c.*) are exceedingly irregular in distribution and widely scattered; they send out numerous branching threads, some of which extend to the periphery and form the thin protoplasmic layer (*p. l.*) directly beneath the cuticle. The musculature tends to be rather feeble; the circular muscle-fibres (*c. m.*) are arranged in a single layer immediately below the protoplasmic layer. The longitudinal muscle-fibres (*l. m.*) are very much stouter and are less regularly arranged. The rest of the body parenchyma consists of (1) large branching cells with perhaps inter- and not intra-cellular spaces filled with granular fluid (*b. c.*), and (2) large rounded vesicular cells (*v. c.*).

The Alimentary Canal.—The mouth in the middle of the anterior sucker leads into a very short and thin-walled pre-pharynx. The pharynx is small, and passes into a quite exceptionally long œsophagus, which extends backwards to about the level of the hinder part of the posterior sucker. Surrounding the œsophagus there can be seen a few glandular cells, the so-called salivary glands. The two gut cæca are comparatively short, being rather less than half the total length of the body (Figs. II, III). The cells of the gut are set on a basement membrane; those of the œsophagus tend to be somewhat flat, while those of the cæca are sometimes so tall as to leave little lumen. Directly outside the

¹ It is very probable that these structures are an artificial production caused by the action of the reagents employed. *Vide* Braun's "Trematoden," Bronn's 'Thierreich,' Bd. iv, p. 593.

basement membrane are circular muscles, and outside of these longitudinal muscles, thus recalling the condition seen in a Chætopod.

The Reproductive System.—The testes are two large rounded bodies lying ventrally to the gut-cæca. The right-hand one is in front of the left, but nevertheless the slender vasa deferentia are of about equal length, the right one becoming looped upwards as the testis is thrust forwards during development. In the quite young individual the two testes are at the same level (Figs. II and XII).

The vasa deferentia open together into a very large vesicula seminalis, which is a thin-walled sac bent sharply on itself, and leading by a short tube into the protrusible muscular cirrus. The whole structure, including the vesicula seminalis and the cirrus, is enclosed in a muscular sheath, which may be called the cirrus-sac (Fig. III).

In the space between the wall of the sac and the cirrus are large glandular cells (*pr. gl.*), which are supposed to act as prostate gland. The position of the cirrus-sac varies considerably in different individuals. It may be either practically in the middle plane or, more usually, well on the left side; occasionally it is on the right. A similar variation has been noticed by Looss¹ in various species.

The ovary (Fig. V, *o. v.*) is a rounded structure lying nearly centrally in the body. From it there springs a short, wide oviduct, which meets (1) the duct from the receptaculum seminis (*r. s.*), which is a thin-walled vesicle lying to the right of the ovary; (2) the common duct from the yolk-glands; and (3) the uterus. Laurer's duct (*L. d.*) extends from the commencement of the duct of the receptaculum to the external aperture. Its close connection with the receptaculum would seem to indicate that its function is to keep the vesicle clear of waste yolk and cement substance, for otherwise the vesicle might readily become blocked with extraneous matter. At the place of meeting of these ducts there is the usual

¹ Looss, A., "Weitere Beiträge zur Kenntniss der Trematoden-Fauna aegyptens," 'Zool. Jahrbücher (Systematik),' Bd. xii, 1898-9.

shell-gland (*sh. gl.*), consisting of large elongated glandular cells. The yolk glands (*yl. gl.*) are fairly numerous, and cluster around the gut-cæca, but they do not extend beyond them anteriorly. The uterus is narrow at its commencement, but it soon widens and forms a thin-walled tube, which is convoluted to only a very slight extent, and then opens into a muscular vagina with a crescentic external aperture (Fig. II, *o. v.*). The uterus lies wholly in front of the testes, and is exceptionally short when compared with the uteri of the majority of Distomids.

Nervous System.—On each side of the pharynx there is a ganglionic enlargement (Fig. II, *n. sy.*); these are connected together dorsally by a nerve-band, but ventrally there appears to be no commissure, and hence there is not a complete nerve-collar around the pharynx. The nerve-strands passing from the ganglia are typical in their arrangement.

Excretory System.—The flame-cells tend to be situated towards the periphery of the body, and they are very few in number. In Fig. VI is shown one of these structures: the nucleus is very large, and the flagellum, showing its composite structure by being very distinctly striated longitudinally, comes off directly from it: an intermediate piece (*b. p.*), doubtless equivalent to the basal knobs of cilia, is clearly visible. The cytoplasm of the cell is not readily separable from the surrounding parenchyma.

The flame-cell leads into a convoluted intra-cellular tube (*cap.*). The tubes open into a slightly wider duct, which also appears to be intra-cellular. There are only two of these ducts, a right and left, and they run inwards towards the excretory bladder (Fig. II, *m. d.*).

The excretory bladder is of very great size, being about one half the length of the body. It is a muscular sac lined internally by very large cells which generally contain several nuclei. The cells are set on a basement membrane, and their development is variable in different specimens, and frequently they are placed separately from one another, so that they do not constitute a distinct and continuous epi-

thelium (Fig. II, *ex. bl.*). On the basement membrane, between the large isolated cells, there can often be seen nuclei which regenerate fresh giant-cells when required (Fig. X, *n.*). The right and left excretory ducts seldom, if ever, open directly into the cavity of the bladder, but they pass into the substance of one of the large cells (Fig. IX, *m. d.*, and X, 2). In this respect the ducts are comparable to the nephridia of certain Chaetopods, where the external opening is closed by a patch of cells, and the excretory matter is passed out through the body of the cells. The bladder opens to the exterior by a narrow and somewhat tortuous channel, which is lined by a thick cuticle continuous with that covering the body. Around this channel there is clustered a group of elongated glandular cells, which apparently pour some secretion into the exit-duct of the bladder (Fig. II, *gl. c.*).

In specimens preserved in Flemming's solution the large cells lining the bladder contained a variable number of black globules, which disappeared in twenty-four hours if the sections were mounted in xylol balsam, but they were permanent in chloroform balsam. Flemming¹ has observed a similar disappearance of fat, blackened by his solution, both by means of turpentine and xylol. We may conclude that the black globules consisted of a fatty substance, which was presumably waste excretory matter.

Correlated with the relative paucity of excretory tubules and flame-cells it is extremely probable that the epithelium of the bladder can itself directly absorb waste matter from the surrounding parenchyma, for it is scarcely possible that the minute main ducts opening into the substance of a couple of cells could convey into the whole epithelium the large quantity of waste products which it undoubtedly contains. The relative thinness of the muscular coat would render easy such a direct absorption of nitrogenous waste.

The Encysted Animal.—It was mentioned above that the trematode commonly lives encysted in the muscles of the

¹ Flemming, 'Zeit. f. wiss. Mik.,' 1889, p. 39.

crayfish. In this condition the animal is bent on itself to form a globular body, and the ventral surface is outermost (Fig. VII). The cyst-wall is of variable thickness, and its mode of formation is peculiar. In sections through the encysted animal there can be seen in the spaces between the parasite and the cyst-wall rounded cells (Figs. VII, VIII, *ex. cl.*) containing two or more nuclei; these cells have passed out from the excretory bladder. The loose cells disintegrate in time into a reticular nodulated material which stains deeply (*f. mt.*). The parasite is constantly rotating inside its cyst, and the disintegrated substance, or even the cells themselves before breaking up, are gradually flattened against the inner surface of the cyst, and increase its thickness (Fig. VIII, 2, *ex. cl.*). It is probable that the greater part, if not the entire substance of the cyst-wall is built up out of such discharged excretory cells.

The cyst-wall frequently exhibits a distinct stratification (Fig. VIII (2), *st.*¹⁻³). The middle stratum (*st.*²) appears to be the densest, and it stains more intensely than the other two layers.

It would be exceedingly interesting to know whether generally the cysts of trematodes which are permanently encysted in the adult state originate in a similar manner. The cysts so often produced by cercaria, and that formed in the developing stages of *D. cirrigerum*, are clearly not formed in this way; they are true cuticular cysts formed by the activity of certain cystogenous cells. It is very possible, indeed, that such a true cuticular cyst would be unfitted for enveloping a growing animal, it not being sufficiently elastic or permeable to nutritive fluids.

The cells of the bladder bud in a remarkable manner (Figs. IX, X), and to a certain extent resemble the yellow cells of the intestine of the earthworm. The structure of the cytoplasm varies considerably in the different individuals examined; probably this is due to the bladders being in different physiological conditions at the time of fixation.

The cytoplasm may present a more or less granular appearance with a few globules of blackened fat.

In other specimens the cytoplasm is richly vacuolated, and the walls of the vacuoles stain intensely. This gives the appearance of sharply defined, deeply stained curved fibrils embedded in a homogeneous stroma. Only by very careful observation under high powers have I been able to be convinced that the apparent fibrils owe their existence to the fact that the walls of the vacuoles stain with unequal intensity (Fig. X (1), *f.*).

Sometimes the vacuoles are of a larger size, and may be seen to contain a granular substance (Fig. X, (3) *v.*₁, *v.*₂). In other bladders every large cell contains one or more very large vacuoles filled with the same granular material (4, *v.*₃); doubtless they are formed by the fusion of the smaller vacuoles. Lastly, excretory sacs occur where the cells have the large vacuoles more or less completely empty, and the contents have apparently passed out into the cavity of the bladder (5, *v.*₄). The globules of fatty matter appear to be more abundant at the time the large vacuoles are formed, but they are not confined to this period (Fig. X, cf. Band 43).

The cells of the bladder would seem to proliferate rapidly both by budding and by the upgrowth of fresh cells from the basal membrane; they become quickly effete, probably by being overcharged with waste nitrogenous substances which they are unable to eliminate sufficiently quickly. The cells break away from the basal membrane and lie loose in the cavity of the bladder; from there they are squeezed out by the contractions of the excretory bladder into the space between the animal and cyst. They now disintegrate, and are plastered against the inner surface of the cyst to increase the thickness of the cyst-wall.

The whole of the phenomena must be regarded as the utilisation of waste nitrogenous matter, and this is analogous to the view that the exo-skeleton of Arthropods is ultimately derived from such waste.

THE DEVELOPMENT OF *D. CIRRIGERUM* IN THE CRAYFISH.

The Egg.—The eggs are very small, and pass out from the uterus into the space between the body and the cyst-wall. The encysted animal appears to die after the formation of the eggs, and the cyst-wall ultimately breaks and liberates the eggs.

The egg-shell is thin and of a dark brown colour; it is very frequently flattened, and shaped like a convexo-concave lens, which is perhaps due to shrinkage; its average length is .012 mm., and breadth .008 mm. Viewed from the convex or concave surface, or even in edge view, the egg is seen to taper towards one end where there occurs a dark-coloured thickened nodule. At the other end, which is rounded, there can be seen the operculum which is doubtless pushed out when the embryo hatches (Fig. XI, 1).

Inside the egg-shell there can be distinguished the egg-cell with a somewhat irregular outline, and surrounding it are a dozen or more yolk-cells containing globules of yolk.

Segmentation.—The egg-cell divides into a number of blastomeres (fig. 2), and at the same time the yolk is gradually extracted from the yolk-cells, which soon appear as flattened cells between the large spherical blastomeres. The nuclei of the blastomeres only stain with great difficulty, while the flattened nuclei of the yolk-cells stain very readily. In this condition the embryo apparently emerges from the egg-shell, but I have not seen an embryo in the act of hatching.

Sporocyst Stage.—The embryo, which may now be termed a sporocyst, consisting of a few quite irregularly arranged blastomeres and flattened yolk-cells, works its way into the thin sheets of connective tissue around the muscles, testis, nerve-cord, etc., and it may acquire a slightly reddish or brownish tint (fig. 3).

The sporocyst, which is generally more or less spherical, now grows considerably, and it may send out many buds consisting of one or several blastomeres. Some of these buds may be

come quite separated from the parent sporocyst, and will produce new sporocysts (figs. 4, 5). At other times a sporocyst may apparently divide by fission into two (fig. 7).

The blastomeres, which appear to have no definite arrangement whatever in the embryo, next divide into numerous small cells (fig. 6), and there is produced a thin irregular cuticular covering which cuts off all outside buds, and puts an end to any further multiplication. Thus the sporocyst now consists of an apparently homogeneous mass of very small cells enclosed by a thin cuticle.

The sporocyst becomes somewhat bean-shaped, and the first sign of differentiation among its minute cells is the formation of a transversely disposed tract of cells in the neighbourhood of the hilum. This tract, shown in section in figs. 8 and 9, becomes cut off by a membrane from the surrounding cells, and some sign of a lumen soon appears. It was at first thought that the structure thus formed was the endoderm, but such is not the case, for it is the beginning of the cirrus-organs, while the gut originates at a later period, and is not produced from these cells. This fundament, however, is often not produced until after the thick cyst-wall, to be mentioned below, is formed.

The outermost cells of the embryo in contact with the thin irregular cuticle appeared, with the most careful observation, to be identical with the cells further in; or, in other words, there is at this period no differentiation into either ectoderm or endoderm.

The sporocyst becomes compressed and convexo-concave, and there is formed a very thick cyst-wall (fig. 10, *c. cy.*) within the original thin irregular cuticle. In some parts of the embryo this cyst-wall may be formed at some depth within the body, so that some of the outer cells of the sporocyst become cut off completely from the cells within the cyst. This process is not sufficiently regular to be regarded as the casting off of the ectoderm, for on one side of the embryo the cyst-wall may be in contact with the irregular cuticle, while on the other side it may be separated from it

by several rows of cells (fig. 10, *e. c.*), and often the cyst encloses all the cells, so that none are excluded from further development.

Cercaria Stage.—The embryo enclosed by the thick cyst will produce the young Distomum, and it may perhaps be regarded as a cercaria, and the cyst as a cercaria-cyst. Scattered through the body there can be seen small clumps of deeply staining cells. After the cercaria-cyst is completely formed they seem to disappear, and I believe they are cystogen glands which secrete the substance which forms the thick cyst (fig. 10, *cy. c.*). Further differentiation now sets in. Around the transversely placed tubular structure above described the cells of the embryo become elongated and stringy in appearance (fig. 10, *m. c. s.*), and they do not stain at all readily with hæmatoxylin. The fundament thus produced will form the muscular cirrus-sac and the structures which lie within.

Reference to fig. 10 will show that there is still no differentiation of an outer layer into an ectoderm, neither has the fundament of the gut appeared.

Body Covering and Cuticle.—The outermost cells of the cercaria never form an epithelium, for they are quite irregularly disposed, and are indistinguishable from the cells below. These outermost cells, however, now fuse together, and produce a thick outer layer of substance that stains like protoplasm. The nuclei of the cells are not included in this outer layer of protoplasm, but lie either just on the inner side of it or are connected with it by strands of protoplasm (Fig. XIV). This outer layer of modified protoplasm may be called cortex, and it is from this that the future cuticle and spinelets are produced (Fig. XV).

The remainder of the cortical substance (Fig. XV, *r. cor.*), after the cuticle is formed, would appear to persist as the thin layer of protoplasm which may be observed in the adult immediately below the cuticle (Fig. XVI, *p. l.*), and connected with the cortical cells by means of branching strands of protoplasm. These cortical cells are the so-called epidermal cells (*ep. c.*).

At one end of the embryo (Fig. XI, 11) the cortical substance is continued inwards into the body, and ultimately the layer splits, and thus there is formed an embryo bent sharply on itself, with its future dorsal surface outermost (fig. 12). This band which splits to form the ventral surface should be regarded as arising by a differentiation of the cells within the embryo, and not as an ingrowth of the outer cortex. The cortical layer now produces the relatively thin definitive cuticle, which is very symmetrically studded with rows of very tiny spinelets (Fig. XV). It is difficult at first to imagine how these structures originate. They are far too small for one spinelet to be produced by one subjacent cell; and further, the cells below the cortex never appear to be arranged in rows or in any way symmetrically. It would appear that the longitudinal and transverse rows of spinelets are produced by the cortex protoplasm as a whole, and not by the sum of the individual efforts of separate cells.

Such an example warns us against regarding the body of an organism as a community of individual units working together for the common good; but it points rather to the conception of the body as a single machine of very great complexity.

The oral and ventral suckers next become distinguishable as two nearly hemispherical bodies, composed of elongated cells with large nuclei.

The ventral sucker is formed at the bottom of the sheet of cortex, which has not as yet split to form the future ventral surface of the animal (Fig. XI, 11).

Formation of the Gut.—At this period in the development the gut-cæca and pharynx become distinguishable. The gut-cæca are formed from flattened cells (Fig. XI, 11, *cæ.*) which apparently become differentiated out of the general cells of the embryo, as I have been quite unable to demonstrate the previous existence of an endoderm. On the right and left of the embryo flattened cells become so arranged as to form a very thin-walled and narrow sac on each side (Fig. XVIII, *cæ.*). The pharynx is seen at some little

distance below the oral sucker, and it is produced from two lateral plates of thick cells which appear at the place where the embryonic gut-cæca come into contact (Fig. XI, 12; Fig. XVIII, *ph.*).

At this time the oral sucker is imperforate, but later the fundament of the pharynx becomes connected with it by a solid strand which ultimately splits and forms the mouth and pre-pharynx. No œsophagus is formed until a much later period after the animal has escaped from its cercaria-cyst.

Gonads.—At this stage three compact masses of cells become visible by reason of their great staining capacity; the mass between the fundament of the cirrus-sac and the ventral sucker will become the ovary, and the two larger masses further behind of a somewhat elongated shape are the embryonic testes (Fig. XIII, *ov.* and *t.*). Later on the testes become globular, and the right-hand one becomes pushed forwards.

The genital atrium originates as a deep invagination of the cortex at the anterior face of the depression of the ventral sucker. Thus at first the genital atrium opens into the pit of the sucker (Figs. XII, XIII, *g. at.*), but later it becomes pinched off from it, so that in the adult the genital atrium opens independently immediately in front of the sucker. The embryonic genital atrium is lined by the general cuticle, studded with spinelets.

The fundament of the cirrus-sac and organs contained therein, lying obliquely across the embryo, becomes narrow at the right-hand end, bends sharply on itself, and extends towards the genital atrium, but as yet it does not open into it. This narrow portion will form the future cirrus and the part of the sac immediately around it (Fig. XIII, *c.*).

A solid band of cells can now be found passing from the ovary towards the genital atrium. This will become hollowed out into a tube, and will form the oviduct, the uterus, and the vagina (Fig. XIII, *f. ut.*).

Clumps of large granular cells containing refringent granules may be seen scattered about towards the posterior

end of the embryo. These later on, when the animal is emerging from the cercaria-cyst, are arranged in two irregular longitudinal lines, and in a transverse line a little below the level of the ventral sucker. They become the yolk-glands (Fig. XII, *yl. gl.*).

Excretory System.—At the posterior end of the body there is differentiated a V-shaped tract of cells with the apex touching the cortex. The tract becomes split, and forms a V-shaped vesicle (Figs. XII, XIII, *ex. bl.*).

The cortex also splits and the general cuticle is continued inwards, so as to line the exit-aperture of the bladder. As the animal grows the exit-aperture lengthens and forms the tortuous channel lined by thick cuticle which occurs in the adult. The cells of the bladder at the time the embryo emerges from the cyst are quite flat. Even at this early period a few perforated cells can be found; these are destined to form the intra-cellular ducts, but flame-cells could not be identified.

The general body parenchyma consists of vesicular cells and branched cells.

The muscular cirrus-sac expands greatly, and the enclosed sac of flat cells forms the vesicula seminalis, the exit-duct, and the cirrus.

Nervous System.—The nervous system commences its development as three small collections of cells, one on each side of the pharynx, and one dorsal to it. The cells mostly produce fibrous elements; the number of ganglion cells formed is very few. The lateral masses become the cerebral ganglia, and the dorsal mass forms the dorsal commissure (Fig. XVIII, *c. g., d. c.*).

Laurer's canal can now be identified as a very thin duct running out to the dorsal surface. The cortical layer of protoplasm becomes relatively much thinner, and the cuticle with spikelets regularly arranged becomes thicker. The cells which produced the cortex become the so-called epidermal cells. Between these cells long thread-like cells with flat-

tened nuclei are formed; these will be converted into the musculature of the body-wall (Fig. XV, *m. c.*).

The embryo, which may be regarded as a fully developed, tailless, encysted cercaria, bursts out of its cyst by straightening itself from its bent position. It now leaves its cyst and burrows between the muscle-fibres of its host. In this position it rapidly grows and soon becomes surrounded by a cyst-wall, which stretches as the animal grows, and is constantly being added to by the addition of fresh matter from the bladder.

Systematic Position.—The enormous genus *Distomum* has been recently split up by Looss into numerous sub-families and genera. According to this author's system *D. cirrigerum* would appear to belong to the sub-family *Lepodermatinae*, and is not very far removed from the genus *Astia*. The characteristic points given by Looss for the sub-family *Lepodermatinae* are—the presence of scales; the excretory bladder lies behind the shell-gland; copulatory organs are well developed; the testes lie in the middle of the hinder portion of the body; the ovary lies close to the blind end of the cirrus-sac; the convolutions of the uterus are sometimes not very numerous, and then they lie wholly in front of the testes.

D. cirrigerum agrees with these general characters. It also resembles *Astia* in the great length of the œsophagus, but it differs from it in a number of ways: the excretory bladder is rounded, and is not forked as in *Astia*; but in the embryo we have seen that it is obviously V-shaped; the uterus is relatively short, and lies in front of the testes; the receptaculum seminis is well developed; the yolk-glands extend beyond the gut-cæca to the posterior end of the body.

Looss mentions that he finds dark granules in the excretory bladder of *Astia*; it would be interesting to know whether they are fatty in nature and are similar to those which have just been described in the excretory cells of *D. cirrigerum*.

On account of the many important differences *D. cirrigerum* could not conveniently be placed in the genus *Astia*, and I would suggest that it should be placed in Looss's system under the name *Astacotrema cirrigerum* (v. Baer).

THE RELATIONSHIP BETWEEN THE SIZE OF CELL AND THE SIZE OF ANIMAL.

In studying the growth of the tissues and organs a question arises which is seldom or never considered, as to the relative sizes of the cells in a young and adult animal. Do the cells maintain the same mean size in the young as in the full-grown animal? *A priori* it might be considered probable that growth would imply simply an increase in the number of cells, and that the mean size of the cells would remain constant throughout.

If, however, we compare Figs. XV and XVI, it can be seen that the nuclei of the young animal have a diameter only about a quarter that of the nuclei of the full-grown adult, also in individuals which are larger but not full-grown the nuclei are of an intermediate size. Hence during a certain period of growth we may expect that the size of the cell is a definite fraction of the size of the animal.

As a rough test three encysted animals were taken, measuring .70, .30, and .17 mm. in diameter; the diameters of twelve nuclei of epidermal cells were measured in each individual, and the means were 11μ , 6μ , and 3μ respectively. Thus quite clearly as the animal grows the nuclei become larger.

Wishing to confirm this result on fresh material, some fourteen *Daphnia* of varying sizes were taken at random from a tank, and the maximum diameters of twelve consecutive epidermal cells were approximately measured in each individual by the following method. The surface of the carapace is covered with a sculpturing consisting of regularly arranged polygonal areas. In a carefully stained animal the nuclei of the underlying epidermal cells can be seen, and as a rule one nucleus occurs under the centre of each polygonal area; accordingly the polygonal areas correspond to cell outlines. Occasionally two nuclei can be seen under one of these areas, but it is not of very frequent occurrence, and since it was found as often in young as in older animals the fact that

an area may sometimes correspond to two cells instead of one will not affect the relative results.

The maximum diameters of a row of twelve areas were measured, and about the fifth row from the ventral edge of the carapace was selected in every case. The results of the measurements are shown in the following table; the means of the twelve measurements are given in the second column.

Length of individual in millimetres.		Mean of 12 measurements in '001 mm.	
mm.		μ	
·9	21·8
1·1	23·0
1·2	24·2
1·3	28·0
1·4	26·4
1·5	25·8
1·7	26·8
1·7	26·9
2·3	32·3
2·5	34·9
2·8	29·0
2·9	35·4
3·0	35·9
3·1	35·5

A similar relationship between the size of the body and the size of its constituent cells was exhibited by some specimens of *Leptodora* which had been mounted whole in glycerine.

Length of <i>Leptodora</i> in millimetres.		Mean of twelve epidermal cells from first joint of endopodite of Ant. ii.	
		Diameter of cell.	Diameter of nucleus.
		μ	μ
·6	...	5·1	...
2·6	...	9·4	...
5·0	...	12·2	...
			3·1

Length of <i>Leptodora</i> in millimetres.		Mean of twelve cells from the middle of the proctodæum.		
		Diameter of cell.		Diameter of nucleus.
		μ		μ
1.3	...	5.4	...	2.9
3.0	...	11.1	...	4.5
7.7	...	14.4	...	5.8

Very probably, in some cases, the size of cells diminishes as the body grows; for example, the red blood-corpuscles of large tadpoles appear to be somewhat smaller than those of small tadpoles.

These few examples which have been brought forward would seem to indicate that the mean sizes of the cells are some definite fraction of the size of the body, and that according to the growth of the body as a whole, so these means may either rise or fall. If such a law of growth be established it lessens our appreciation of the individuality and relative independence of the cell units, and it would weaken the view which regards the body as a cell-republic. A thorough statistical investigation into the subject would be of much interest, and the results might lead to a great modification of the current views as to the profound importance of the cell. In a future publication I hope to enter into greater detail.

SUMMARY.

The material available for the present investigation was quite inadequate for elucidating the life-history of the species. The only new fact added is the discovery that the sexual form can develop from the egg in the crayfish itself; hence, were it not for the problematical *D. isostomum* we should regard the trematode as monogenetic, and having a quite simple life-history. The formation of a cercaria-cyst would indicate, however, that this monogenetic character was secondarily acquired, and that at some former time it was typically digenetic.

The occurrence of the sexless *D. isostomum* in the crayfish complicates the problem, and if Zaddach is correct in regarding this sexless form as arising from the eggs of *D. cirrigerum*, it would follow that either the sexual or the sexless form can be produced in the crayfish according to circumstances. In my numerous sections there occurred one remarkable individual which cannot altogether be understood. It was embedded in the superficial substance of the testes, and apparently had developed in this position from the egg. It was not enclosed in a cyst, and had no appreciable cuticle. It differed from the usual form in having no obvious trace of generative or copulatory organs. From a solitary specimen found in section it is scarcely safe to speculate, but its structure is certainly suggestive that it would have developed into *D. isostomum*.

The chief peculiarity in the structure of the species is the remarkable excretory epithelium of the bladder. The epithelium consists of very large cells which apparently are capable of extracting waste matter direct from the surrounding parenchyma, since the excretory tubes are few and small. The cells are able to bud; after a period of activity they become effete and are passed out of the bladder. Ultimately they disintegrate and add to the thickness of the cyst-wall. Fresh cells are produced in the bladder from reserve nuclei lying on the basal membrane.

The animal grows to maturity permanently enclosed in a cyst, hence the cyst-wall must be highly elastic and permeable to nutritive fluids. I believe that most, if not the entire substance of the cyst-wall, is derived from the worn-out excretory cells.

Laurer's duct comes off in close connection with the receptaculum seminis, as if for the purpose of keeping this vesicle free from waste yolk and cement substance. The position of the cirrus-sac varies considerably in different individuals. I have not observed the act of self-copulation.

According to Looss's system the present *Distomum* may be referred to the sub-family *Lepodermatinæ*, and it is placed

in the new genus *Astacotrema*, not very far removed from *Astia*.

The development of the sexual form presents some features of theoretical interest in connection with the doctrines of heredity and of the germ-layers. The irregular and apparently erratic nature of the development is very surprising. An embryo consisting of a few loose blastomeres and yolk-cells escapes from the egg-shell. Nothing of the nature of a "hyaline membrane" or the stripping off of an outer layer of flat cells could be detected. The whole embryo may or may not fall to pieces, so to speak, and the separated blastomeres are able to develop into the mature animal. More usually the embryo grows to a considerable size, and then it may or may not send out buds consisting of one or several blastomeres with perhaps a few yolk-cells attached. These buds do not necessarily develop; they may degenerate and form a more or less continuous sheath around the central developing embryo. The blastomeres remain of a considerable size during the earlier stages of division and budding. Next the blastomeres divide into quite small cells, and the embryo becomes oval in outline, and ultimately somewhat bean-shaped, and a thin irregular cuticle is produced. Even at this advanced stage the embryo may apparently divide by fission into two. The whole embryo consists of an apparently perfectly homogeneous mass of small cells. There is next secreted a very thick cyst-wall, which is sometimes, although not always, produced at some little distance within the body of the embryo. On account of the erratic nature of this outer layer, which is by no means always formed, it is very doubtful if it should be regarded as ectoderm. Clearly the cells which become enclosed by the new cyst will alone form the embryo, and therefore up to this period the general cells of the embryo are not predestined to form any particular part of the future body. The fundament of the vesicula seminalis and surrounding cirrus-sac may, however, sometimes appear even before the thick cyst is formed.

At first the cells of the embryo in contact with the thick

cyst-wall are indistinguishable from those lying deeper. After a time there is formed an outer layer of apparently modified protoplasm; the nuclei of the cells which have produced it lie on the inner side and are quite irregularly disposed, and may be connected with it only by strands of protoplasm. These cells become the epidermal cells of the adult.

The course of development after the thick cercaria-cyst is formed may be briefly recapitulated in the following paragraphs:

(1) The cortex-protoplasm secretes a thin cuticle studded with very symmetrically arranged spinelets.

(2) The fundament of the cirrus-sac becomes a thick-walled muscular tube enclosing the embryonic vesicula seminalis, and it lies obliquely across the embryo.

(3) The cortex is continued upwards by differentiation from one end of the embryo; this will split, and will constitute the ventral surface of the future adult.

(4) Oral and ventral suckers are differentiated.

(5) The gut-cæca are formed from very flat cells, which become arranged into a right and left vesicle, meeting at the fundament of the pharynx.

(6) Fundaments of the gonads appear.

(7) The genital atrium is formed as a deep pit, which opens at first into the depression of the ventral sucker.

(8) The fundament of the cirrus-sac is continued forwards to the genital atrium, but does not as yet open into it. The fundament of oviduct, uterus, and vagina appears as a short tube running from the ovary to the atrium.

(9) A strand is formed passing from the pharynx to the oral sucker; this splits, and thus the mouth and pre-pharynx originate.

(10) The excretory vesicle is formed as a V-shaped tract, which splits into a V-shaped, thin-walled vesicle opening to the exterior by a pore lined by the general cuticle.

(11) The intra-cellular ducts of excretory system are formed. Yolk-glands appear.

(12) Embryo escapes from its cercaria-cyst.

(13) Embryo burrows into the muscles of its host. Œsophagus is formed, and excretory exit-duct elongates and becomes tortuous, and the cluster of glandular cells around it are developed. The V-shaped excretory bladder becomes globular.

The interpretation which may be given to these observations will vary according to the preconceptions of the observer, and on the definition given to the term "germ-layers." A germ-layer may be defined as a mass or layer of cells which is differentiated from the rest of the body quite early in embryonic life, and out of which certain organs and these alone are produced. From the point of view that ectoderm, endoderm, mesoderm, and fundament of gonad are morphologically homologous parts throughout the animal kingdom it would appear extremely doubtful whether in the present development a true ectoderm or even a true endoderm is formed. The cortex is produced simply by the outermost undifferentiated cells of the embryo which persist in the adult as the "epidermal" cells.

If, however, the "germ-layer" is merely a physiological conception of the relative relationships of different layers of the embryo there is nothing against calling the cortex-producing layer ectoderm, for then the term bears no meaning except that it is the layer of the embryo in contact with the surrounding medium.

It should be remembered, however, that the development of the present embryo is obviously a much abbreviated one. This is clearly shown by the curious splitting of the inner sheet of cortex to form the ventral surface, and also by the early appearance of the fundament of the cirrus-sac. But the general tendency of recent embryological work is certainly in the direction of weakening and not strengthening the conception of the morphological significance of germ-layers; for example, the budding of certain tunicates from the ectoderm alone, the budding of medusæ from the ectoderm of the manubrium (e. g. in *Margellium*), the apparent formation of a part of the nervous system in echinoderms from cells which

are clearly not ectodermal, and a number of other cases could be cited.

From the course of development previously described it can be seen that the hereditary tendencies can be passed on unimpaired through a considerable amount of budding, and then after the blastomeres have divided into quite small cells it seems to be a matter of indifference how many of them are enclosed in the thick cercaria-cyst; the excluded cells perish, the enclosed mass will develop into the embryo. Hence up to this period there is no sorting out of hereditary tendencies (except that sometimes the fundament of the cirrus-sac appears quite early) into separate cells, but they reside in the mass as a whole as they would in the body of a protozoon, and are not separated out into distinct elements. The mass of cells enclosed by the cercaria-cyst and beginning its development should be regarded as an unit, and not as a cell-republic.

However special and obscure this development may be held to be, yet the very fact that such a mode is possible, in that the various organs appear direct in the homogeneous mass of cells without the intervention of germ-layers, seems to the author to demonstrate, in the words of Sachs,¹ that "cell formation is a phenomenon very general, it is true, in organic life, but still only of secondary significance; at all events, it is merely one of the numerous expressions of the formative forces which reside in all matter,—in the highest degree, however, in organic substance."

THE EXPLANATORY ABBREVIATIONS.

ap. ? aperture of flame-cell. *b.* Section of the body of the encysted animal. *b. c.* Branched cells. *b. p.* Basal portion of the flagellum. *bd.* Bud from sporocyst. *bm.* Blastomeres. *c.* Cirrus. *c. g.* Cerebral ganglion. *c. cy.* Cercaria-cyst. *c. m.* Circular muscle. *c. s.* Cirrus-sac. *c. v. s.* Cells to form vesicula seminalis. *c. w.* Cyst-wall. *cav.* Cavity of flame-cell. *cæ.* Gut-cæcum. *cor.* Cortex. *cy.* Adult cyst. *cy. c.* ? cystogen cells of embryo.

¹ Sachs, Julius von, 'Lectures on the Physiology of Plants,' translation by H. Marshall Ward, 1887, p. 73.

d. c. Dorsa commissure. *d. r. s.* Duct of receptaculum seminis. *e. c.* Excluded cells of embryo. *eg.* Egg. *eg. c.* Egg-cell. *ep. c.* So-called epidermal cells. *ex. c.* Excretory canal. *ex. cl.* Excretory cell from bladder. *ex. bl.* Excretory bladder. *e. i. c.* Eggs in cyst cavity. *e. i. u.* Eggs in uterus. *f.* Apparent fibrils in excretory cells. *f. mt.* Formative material for cyst. *f. ut.* Fundament of uterus. *fl.* Flagellum of flame-cell. *g. at.* Genital atrium. *gl.* Osmicated fat globules. *gl. c.* Gland-cells at exit-duct of bladder. *i. cor.* Cortex which splits to form the ventral surface. *i. cy.* Irregular cuticle. *l.* Lid of egg-shell. *L. d.* Laurer's duct. *l. m.* Longitudinal muscle. *m. c.* Developing muscle-fibres. *m. c. s.* Muscle-cells for cirrus-sac. *m. d.* Main duct of excretory system. *m. f.* Muscle-fibres. *m. h.* Connective-tissue surrounding muscles of the host. *n.* Nucleus of reserve cell of bladder. *n. sy.* Nervous system. *n. d. c.* Nucleus of disintegrating excretory cell. *nu.* Nucleus of flame-cell. *n. y.* Nucleus of yolk-cell. *o. s.* Oral sucker. *o. v.* Opening of vagina. *œ.* Esophagus. *ov.* Ovary. *ovid.* Oviduct. *p.* Body parenchyma. *ph.* Pharynx. *p. ph.* Pre-pharynx. *pl.* Protoplasmic layer under cuticle. *pr. gl.* Prostate gland-cells. *pr. t.* Prostate tube. *r. s.* Receptaculum seminis. *r. cor.* Remainder of cortex. *sh. gl.* Shell-gland. *sp.* Cuticle with spinelets. *st.¹ st.² st.³* Strata of cyst wall of adult and of cuticle. *t.* Testis. *t. h.* Testis of host. *ut.* Uterus. *v.₁* Small vacuoles in excretory cells. *v.₂* The small vacuoles collected into larger vacuoles. *v.₃* Great vacuoles full of granular contents. *v.₄* Emptied vacuoles. *v. c.* Vesicular cell. *v. s.* Vesicula seminalis. *vt. s.* Ventral sucker. *y. c.* Yolk-cell. *y. d.* Yolk-duct. *yl. gl.* Yolk-gland.

EXPLANATION OF PLATES 24—26,

Illustrating Mr. Ernest Warren's memoir on "Distomum Cirrigerum, v. Baer."

FIG. I.—× 20. The free animal from the side, viewed as an opaque object.

FIG. II.—× 88. The free animal from the ventral surface, viewed as a transparent object.

FIG. III.—× 33. The free animal from the side, viewed as a transparent object.

FIG. IV.—× 33. An encysted animal in the act of escaping from its cyst. Eggs may be seen inside the cyst.

FIG. V.—× 100. The female generative organs, semi-diagrammatic, constructed from serial sections and viewed from the side. Notice the close connection of Laurer's duct with the receptaculum seminis.

FIG. VI.— $\times 1440$. A flame-cell with the convoluted capillary duct. The cytoplasm of the flame-cell is not separable from the general protoplasmic reticulum of the body (*p.*). The composite origin of the flagellum is indicated by the distinct longitudinal striation, and the intermediate piece between the nucleus and the flagellum is well seen (*b. p.*). A possible aperture occurs on one side (*ap.*).

FIG. VII.— $\times 40$. An encysted animal, viewed as a transparent object. The ventral surface is outermost. Eggs and excretory cells can be seen in the space between the body of the animal and the cyst-wall.

FIG. VIII (1).— $\times 160$. Section through the edge of a cyst. The space within is the cavity of the cyst between the small portion of body (*b.*), cut through, and the cyst-wall. In the space are shown excretory cells in the process of disintegrating into the nodulated material (*f. mt.*), which becomes plastered against the inside of the cyst-wall, and increases its thickness.

(2).— $\times 320$. A piece of the cyst-wall under greater magnification. In the upper portion an excretory cell is being flattened against the inner surface of the cyst, while below the more usual disintegrated substance can be seen.

FIG. IX.— $\times 225$. The upper portion of the excretory bladder, with the right and left main ducts opening into the lining epithelium on each side.

FIG. X.— $\times 200$. Excretory epithelia from the bladders of five individuals.

- (1) Shows the apparent fibrils (*f.*) and a few osmicated globules of fat.
- (2 and 3) The cells possess many vacuoles which are collecting into larger vacuoles.
- (4) The cells generally possess one large vacuole with granular contents. In the lower part of the figure can be seen a cell in the act of budding.
- (5) The large vacuoles have become emptied.

FIG. XI.— $\times 250$. Various stages in the development of the sexual form.

- (1) Egg in side view showing egg-cell (*eg. c.*) and yolk-cells.
- (2) Segmentation has occurred, producing a number of large blastomeres with badly staining nuclei.
- (3) The sporocyst embedded in the superficial substance of the testis of the crayfish; the general arrangement of the blastomeres appears quite irregular. The yolk-cells are becoming flattened (*n. y.*).
- (4) A budding sporocyst in surface view.
- (5) A budding sporocyst in surface view.

- (6) Section of sporocyst after budding is completed. The blastomeres have divided into small cells possessing nuclei, which stain with great difficulty. No yolk-cells are now visible.
- (7) A sporocyst in surface view, dividing by fission into two.
- (8) Sporocyst in section; it becomes bean-shaped, and a delicate irregular cuticle is produced. The fundament of the male copulatory organs may appear. Often, however, it is not formed until later.
- (9) The irregular cuticle becomes thicker.
- (10) Cercaria-cyst is formed, and embryo is seen in longitudinal section. The cyst may be produced at some little depth within the embryo, and hence some of the cells of the embryo become excluded from the future development (*ex. c.*). The fundament of the male copulatory organs has increased. Perhaps cystogen cells occur (*cy. c.*).
- (11) Cortex is formed, gut appears, also suckers and gonads.
- (12) The embryo in longitudinal section, showing the final stages of development. The inner sheet of cortex has become split to form the ventral surface; cuticle with spinelets is produced by the cortex.

FIG. XII.— $\times 280$. The sexual form escaping from the cercaria-cyst. It is viewed ventrally and as a transparent object. Notice the symmetrical arrangement of the spinelets, the genital atrium opening at first into the depression of the ventral sucker and the V-shaped excretory bladder.

FIG. XIII.— $\times 400$. Embryo in longitudinal section nearly ready to emerge from cercaria cyst. Notice genital atrium, cirrus, uterus, and the origin of the excretory bladder.

FIG. XIV.— $\times 880$. A small piece of the cortex with the underlying cells of an embryo soon after the cercaria-cyst is formed.

FIG. XV.— $\times 880$. A small piece of a somewhat older embryo; the underlying cells become differentiated into "epidermal cells," muscular cells, branched and vesicular cells. The thin cuticle and spinelets are produced.

FIG. XVI.— $\times 400$. Transverse section of the adult. The cuticle is raised into scales, but no spinelets were visible. The thin layer of protoplasm (*pl.*) under the cuticle is the remainder of the embryonic cortex. A few circular and longitudinal muscle-fibres are visible.

FIG. XVII.— $\times 400$. Longitudinal section to show curious inflated structures, which are probably an artificial production.

FIG. XVIII.— $\times 400$. Transverse section of the anterior portion of a developing embryo to show the origin of the gut-cæca, pharynx, and nervous system.

Studies in the Retina.

Part VI.—The Continuity of the Nerves through the Vertebrate Retina.

By

H. M. Bernard, M.A.Cantab.

(From the Zoological Laboratories of the Royal College of Science.)

With Plates 27—29.

THIS sixth paper concludes the series.¹ It was my original plan to publish any observations I might be fortunate enough to make which threw light on the general structure of the retina, as introductory to a series of comparative studies on the eyes of different groups of animals, the ultimate object being to accumulate and elaborate the evidence which had seemed to me to point to a mechanical theory of vision.² Whether the original plan will ever be carried out remains to be seen. I express the doubt because the new matter contained in this paper threatens to draw me off into other

¹ Part I appeared in vol. xliii, p. 23; Part II in vol. xlv, p. 443; and Parts III, IV, and V in vol. xlvi, pp. 25, 40, and 48 of this Journal.

² An outline sketch of this theory was given in the 'Ann. and Mag. Nat. Hist.,' xvii (1896), p. 162. Practically the same theory has been recently presented to the French Academy by Professor Pizon, see 'C. R.,' cxxxiii, 1901, p. 835. There are slight differences of detail, but, so far as I can make out, not where Professor Pizon thinks they lie.

and larger fields than the retina. The discovery of continuous nerve-paths through the retina along lines in which no one acquainted with the current views and theories would have thought of looking for them, seems to demand some revision and readjustment of modern doctrines with regard to several important morphological problems. And yet there is not so much that is really new in this paper, for, when critically reviewed, it will be found that nearly every fact has been seen and described by other workers. What the retina has now revealed is not so much new facts as new clues, which will, I believe, enable us to co-ordinate a number of hitherto isolated and, on that account, often neglected observations.

The search for direct continuity between the nerve-strands and the rods of the vertebrate retina, in which rods there is every reason to believe the nerves must terminate, seems in recent years to have been abandoned. The reason is not difficult to understand. The problem had baffled all the leading retinologists of the latter half of last century, and this fact prepared the way for a new theory of nerve action which rendered direct continuity unnecessary. Indeed, the retina became one of the chief witnesses for the intermittent contact theory. My own researches, however, soon convinced me that the phenomena on which the upholders of this latter theory were relying were not to be trusted so far as the retina is concerned. As soon as it dawned upon me that the elaborate series of ganglionic cells with their systems of dendrites, which were supposed to convey the stimulus from the rods to the nerves, admitted of another and much simpler interpretation, I naturally once more took up the quest for the nerve-paths, without, however, any hope of solving a problem which had appeared insoluble. The discovery came, as it were, of itself some three or four years ago in the way described in this paper.

The descriptions of the "ganglionic cells" of the vertebrate retina, as given in the text-books, are familiar to all. Associated with such names as those of Corti, Koelliker, H. Müller,

Remak, Max Schultze, and others, they have been accepted for the last forty years without question. They are represented as multipolar bodies with large vesicular nuclei, each with one proximal process, called the axis-cylinder process, continuous with one of the fibres of the nerve-layer, and one or more distal processes, which plunge into the inner reticular layer, where they ramify and are lost. These processes are all apparently prolongations of the cytoplasm of the cell-body, the conspicuous nucleus, so far as one can see, taking no part in their production. Our knowledge of the finer structure of this cytoplasm, through which we are left to conjecture that the stimulus must pass from the retina into the optic nerve, may be summed up as follows:—It consists of the fibrillar substance of Flemming with the interfibrillar hyaloplasma, further complicated by (1) the presence of the staining clumps ("Nissl's Schollen"), often arranged in irregular concentric rings round the nucleus; and (2) the occurrence of one or more refractive staining globules, "centrosomes," each in the centre of a clear field. Add to these the fact that the nucleus contains a nucleolus suspended on an intra-nuclear reticulum, and we have all the accepted constituents of the ganglionic cells of the retina.

It must be admitted that this familiar diagram seemed to meet some of the needs of the problem as to the passage of the nerve-stimuli, for it at least shows the fibres of the optic nerve bent down at right angles into the retina, i. e. towards the layer of rods. The one great difficulty was, however, to find how the nerves bridged over the interval between the processes of these ganglionic cells, assuming at least one of these processes to be nervous, and the rods. This has been, if I may say so, the burning problem of the retina, viz.: which of the two or three distal processes of the ganglionic cells carried the stimulus? Why were they all, sooner or later, lost to view? Why was not at least one of them traceable right through to the rod-layer? No solution of this problem seemed to be forthcoming until the elaboration of the metal impregnation methods, especially in the hands of

Ramon y Cajal, seemed to clear up the mystery. According to the results obtained by these methods, the fibre of the optic nerve still runs into the "ganglionic cell" as shown in the old diagram, but there is no longer any necessity to trace any single one of the distal processes of the cell through the retina; for direct fibrillar connection with the rods is not required. The new doctrine is that the ramifications of the ganglionic cell within the inner reticular layer are able to receive the stimulus from the rods through the mediation of opposed ramifications of other more distal cells by some kind of intermittent contact.

One of the very earliest results of my own study of the retina, however, was the conviction that the thick cytoplasmic axis-cylinder process joining the ganglionic cell to the optic nerve has no existence. Though during the last ten years I have examined many hundreds of preparations of vertebrate retinas fixed and stained by all the best known methods which are relied upon for ordinary histological work, I have never once been able to see it. In sections cut along the optic nerve it surely ought to have been seen, especially when the distal processes of the same cell were always visible. It was long before I could bring myself to deny the existence of so important an element of the above-mentioned familiar diagram, especially in the face of the direct support which the recent work of Ramon y Cajal, Dogiel, and others appears to lend to it. And, indeed, I did not do so until I had something positive to put in its place. It is now, however, perfectly certain that the appearances which gave rise to the diagram, and still seem to give rise to it, have been wrongly interpreted.

Beginning with the observation which first shook my faith in the correctness of the old diagram, I found that, if we take a survey of the retinas of a number of different vertebrates, only a small proportion of the ganglionic "cells" have any even superficial resemblance to the diagram. It has been constructed almost entirely upon phenomena most frequently found in the Mammalia, and rarely in the lower forms. In

the lower forms, e. g. in the Amphibia, most of the ganglionic nuclei either have no cytoplasm at all, and are simply nuclei, somehow suspended in larger or smaller meshes of the retinal syncytium, or else they have a mere trace of it, usually on their distal sides, and trailing away into the inner reticular layer (see, for instance, figs. 2 *a*, 3 *d*, 18 *d*, the top nucleus). In every case in which cytoplasm does occur in connection with these nuclei it is impossible that it could be overlooked; whatever its real constitution may be, it appears under the microscope as a refractive granular mass, and I shall always refer to it as granular cytoplasm to distinguish it from the smooth, glassy strands of the syncytial supporting framework of the retina. In the vertebrate retina, then, the granular cytoplasm, so essential a factor in the old diagram, is found associated with the ganglionic nucleus in very varying quantities; it shows almost every stage, from the condition in which it renders a reticular chamber in the retinal syncytium turgid, as represented in the diagram, to that in which it is present in the merest traces, or even completely absent. Figs. 1 to 3 and 5 to 12 represent ganglionic "cells" of different vertebrates; such figures might be multiplied indefinitely; those here given are but a very small selection from the number I have drawn under the microscope. Figs. 2 *b*, *c*, 3 *a*, *b*, *c*, and 8 show ganglionic nuclei without any cytoplasm, while, in fig. 12, three nuclei have a certain amount of cytoplasm and the rest not a trace.

Almost at once, then, we are called upon to modify our conception of the retinal "ganglionic cells," as obtained from the familiar diagram, and we must describe them as the innermost layer of the retinal nuclei, which may or may not have a certain quantity of associated cytoplasm. Thus it is obvious that (1) in those cases in which there is no cytoplasm there can be no axis-cylinder process such as that required by the diagram; (2) in those cases in which the cytoplasm is entirely confined to the distal side of the nucleus, the diagrammatic cytoplasmic axis-cylinder process, continuous with a fibre of the optic nerve, is equally out of the question; and (3) even in

the case in which the granular cytoplasm actually surrounds the nucleus, but does not completely fill a syncytial chamber, an axis-cylinder process is difficult to imagine. It is only in the comparatively few cases (few, that is, except in the eyes of the higher vertebrates) in which the cytoplasmic matter completely fills the syncytial chamber (cf. fig. 1, and the majority of the drawings in fig. 26), making it turgid, that the diagrammatic axis-cylinder process is possible. But, in such cases, as stated, I have never yet, in the whole course of my study of the retina, succeeded in finding it, although the distal ramifications from the same cells, when there are any, are always quite distinct.

This is apparently the experience of at least some other workers also. For example, Birch-Hirschfeld¹ has recently published a paper with careful drawings of sections of retinas showing ganglionic cells, but none with the diagrammatic axis-cylinder processes. On the other hand, Borysiewicz figures such processes in the typical manner. And here let me say that there is nothing in the account here to be given of the nerve connections which precludes the possibility of the existence of such processes; indeed, it is a matter of surprise that they do not appear to occur. I am only stating the fact that, during ten years' continuous work on many retinas, I have never seen anything like the diagrammatic axis-cylinder process, though, at one time, I looked diligently for it. I am therefore justified in concluding that when it occurs it is of the nature of an accidental variation upon the ordinary mode of connecting the nerve with the ganglionic cell which will be described below.

Further, the description of the "ganglionic cells" as nuclei, with which granular cytoplasmic matter may or may not be associated, applies to all the "cells" of the retina. It is well known, for instance, that the nuclei of the middle nuclear layer have, as a rule, no conspicuous masses of cytoplasm. A few very large "cells," closely resembling the

¹ 'Arch. Ophth.,' 1 (1901), p. 166; cf. also Abelsdorf's figures in the 'Arch. Augenheilk.,' xlii, p. 188.

typical multipolar ganglionic cells, occur here and there in the higher Mammalia as if abnormally (see, e. g., the figures Nos. 22 and 23 in Borysickiewitz's 'Untersuchungen,' 1887).¹ Again, the nuclei forming the innermost row of the middle nuclear layer along the outer edge of the inner reticular layer, frequently have a slight trace of associated cytoplasm, usually only on their proximal sides, and looking as if it had come through the inner reticular layer and had left a trail running radially into that layer.

Nuclei with such trails of granular cytoplasm, and, perhaps, a few here and there entangled in the Müller's fibres, as explained in Part V, p. 59, are, so far as I can see, the only foundation for the so-called "bipolar ganglion cells" of the middle layer shown in all the diagrams as radially arranged, spindle-shaped cells. So far as my experience goes, these diagrammatic bipolar cells of the middle layer have no more real existence as fixed morphological elements than have the multipolar ganglionic cells described above. The only nuclei of the retina that are suspended in the way shown in the diagram—viz. within a spindle-shaped mass of cytoplasm, which in no case could be the granular cytoplasm we have been referring to, but rather a strand of the syncytial framework—are: (1) those forming the still undifferentiated rim in young eyes (cf. Part III, p. 33, and fig. 24, illustrating this paper); and (2) those forming the outer nuclear layer, or layer of rod-nuclei, when it is several rows thick. With the former of these exceptions, the nuclei of the middle layer of the retina are not only not surrounded by granular cytoplasm, they are not even wrapped closely round by any portion of the syncytial framework nor suspended on strands of the same; but they are somehow supported within the meshes of the retinal syncytium as in so many perinuclear spaces, large or small, according to the age and condition of the eye. How these apparently free nuclei were suspended and

¹ In Petromyzon, the outermost row of nuclei of the middle layer always have a quantity of granular matter associated with them, but these "cells" have no ramifications.

kept in place within such meshes was a puzzle to me which became still more perplexing when, as not seldom happens, the syncytial strands are so scanty that very few can be traced at all, even with the best microscope.

But before coming to this point, let me say that the *à priori* improbability of a tissue with simple nuclei not, as a rule, in direct contact with any cytoplasm, led me to test the observation again and again in every possible way. I have studied small slices of nuclei cut tangentially and isolated in the sections with the highest microscopic powers (cf. fig. 4). I can see nothing in such cases but the frequently angular reticulum of the nucleus. Indeed, I have quite convinced myself that, except for the few that become apparently accidentally involved in the "Müller's fibres" and the spindle-shaped cells at the rim of young retinas, the membranes and strands of the syncytial framework are not normally in contact with the nuclei, but run between them, or if they are in contact, it is of the nature of an accident and due to crowding.¹

This discovery will certainly help to settle certain long-standing differences of observation. The nucleus has always hitherto been thought of as necessarily embedded within a mass of cytoplasm, and such nuclei only have been studied. Any direct connections between the nucleus and its surrounding tissues, if any such connections exist, have been obscured by the enveloping mass of cytoplasm, and the prevailing doctrine is that whatever connections it may have with its surroundings are only indirect, namely, through the intermediary of its own cytoplasm. But now we have a tissue, viz. the retina, in which the majority of the nuclei have no masses of cytoplasm obscuring them, and can be studied by themselves, and their connections, if they have any, can be

¹ In very young eyes the nuclei may be packed so tightly together as to be polygonal (fig. 14); in such cases they must, of course, be in contact with any syncytial framework which happens to be present. As the eye grows older the nuclei move apart from one another, and strands of the supporting framework appear irregularly between them.

made out. This, indeed, is what we shall now do, and, as we shall see, with a result common enough in science, that observations long neglected and discredited, and over which some patient observer perhaps broke his heart, are at last confirmed.

The first clue as to the method of suspension of the retinal nuclei was supplied by a discovery which I made several years ago, but neglected because, at the time, it was too fragmentary even to suggest its being more than some accidental phenomenon. At intervals I noticed exquisitely delicate threads emanating from the intra-nuclear network, one here and there, and running from nucleus to nucleus. They were very difficult to focus, and, no matter how deeply the section was stained, remained hyaline or subtended too small an angle to show any colour. They were at first rarely seen; many slides showed no trace of them, however diligently they were searched. But after finding them in several different eyes, sometimes singly, sometimes three or four close together, I became convinced that they indicated something of importance for the understanding of the retina. Figs. 13 *a* and *b* represent some of the first instances seen. The connecting threads were just on the borders of our best microscopical powers of vision, and so delicate that one could rarely hope, I thought, to find them preserved intact over a large field.

Fortunately we are not confined to evidence so difficult to obtain as this in order to establish the existence of these filaments as a permanent addition to our knowledge of protoplasmic structure. There is an abundance of other evidence, much of it, it is true, indirect, but nevertheless so instructive that I have long given up straining my eyes to try to see the filaments directly. As a somewhat interesting personal experience, however, I should like to add that since this paper was nearly in its present shape I have once more run over a score or two of sections of different retinas for the express purpose of ascertaining whether, now that I have no more doubt as to their existence throughout the whole retina, I

cannot see them more distinctly. I have been astonished at the difficulty experienced; section after section was searched in vain; not a trace of them could be seen, either because they had been ruptured or else because they are so fine that they are easily obscured or otherwise elude our search. Then suddenly a slide showed them perfectly clearly. The chief cause of their visibility will be explained in the sequel. I can no longer wonder at the fact that the few records which have been made from time to time of threads radiating outwards from nuclei in other tissues have, with few exceptions, fallen into discredit, nor that the internuclear connecting filaments of the retina have never been seen before, or, if seen, have been regarded as accidental phenomena.¹ The fact is, on the contrary, it is their preservation, and, even if preserved, their visibility which is accidental. But, in the course of these researches, so many retinas were studied that the accidental apparitions of the internuclear connecting filaments became in time numerous enough, first to suggest their being of importance, and ultimately to convince me of their universal existence as primary factors in protoplasmic tissues.

Let us pass the indirect evidence in review, taking each layer in turn, beginning with the largest.

Evidence for the Existence of the Internuclear Connecting Filaments between the Nuclei of the Middle Nuclear Layer.

1. The nuclei of this layer are frequently found somewhat crowded. If the material is well fixed, i. e. shows the intra-

¹ I should like also to add that a great deal of recent work has been done on the retina, in which more attention has been paid to the staining than to the fixation of the material. The nuclei are seldom shown in the figures with a reticulated internal structure; they are too often mere sacs of disorganised granules. The metal impregnation methods reduce them to mere smudges. The result of my own work convinces me that the missing keys to many unsolved problems will be ultimately found in the finer structure of the nucleus.

nuclear networks, any good microscope will show the continuity of these networks when, as in very young eyes, the nuclei are in contact or almost in contact with one another (fig. 14). The short uniting threads which run from one nucleus into the other are usually very numerous,—the union between their networks being best seen by focussing up and down rather rapidly. But the very short uniting threads in such cases are not like the filaments shown in fig. 13; they are far too thick, and they can only be regarded as filaments coated over with other substances. The fundamental filaments themselves are exquisitely delicate and achromatic. Whenever, therefore, internuclear bridges are seen with comparative ease, what we see are not the fundamental filaments themselves, but other staining substances coating them and probably, as we shall see, streaming along them.

2. In retinas fixed with osmic vapour, the nuclei frequently become blackened homogeneous bodies, having the appearance shown in fig. 17 *c*. Most of them show one or more exquisitely sharp points, frequently traceable into filaments. Here and there, where the nuclei are close together, unbroken filaments connecting them into groups may be detected; and others, which run, not to an adjacent nucleus, but into the inner reticular layer, in order, as we shall see later on, to join some nucleus of the innermost ("ganglionic") nuclear layer, seem to be frequently preserved. I have noted several times that the nuclear filaments that run into and through the spongy reticular layer are less liable to be ruptured than those joining adjacent nuclei, unless the latter are very close together.

3. In specimens fixed with boiling corrosive sublimate, the fixative which first revealed the full length of the cones in the amphibian retina (cf. Part I, this Journal, vol. xliii, p. 23), the nuclei of the middle layer are, in some instances, all balled together as small globules of refractive chromatin with their connecting filaments ruptured; but in others they have responded to the stimulus in the very opposite way, and are changed into amœboid masses with their radiating pro-

cesses uniting them into a network (see fig. 16). Their individuality as nuclei is, however, never quite obliterated, but the union of their processes is so uniform throughout the sections that there is no other conclusion possible than that their chromatin substance must have run out along pre-existing connecting filaments. Here, again, the filaments are made visible by the presence of staining matter upon them.

4. In some of the tadpoles killed at night all the filaments are clotted over with staining matter, as shown in figs. 18 *a—d*, and are then quite visible, sometimes as a tangle, even with moderate microscopic powers. Here, again, the filaments themselves are only seen indirectly owing to the staining matter which coats them.

5. By focussing up and down with a high power rather rapidly, individual nuclei can sometimes be seen to possess a subtle radiation, although it is difficult to focus any particular ray. They have at times reminded me of some small short-rayed Sun-animalcule. At other times, as in fig. 17, *b* and *d*, the rays of some of them become clearly visible—owing, I believe, to their being coated with staining matter.

6. In fig. 17 *a*, the chromatin is contracted into the centres of the nuclei, which, as we shall see elsewhere, is probably a periodical phase passed through by the nuclei alternating with a phase in which the chromatin is diffuse, as in 17 *b*. In figs. 17 *c* and *d*, we see nuclei passing from one phase into the other.¹ The filaments which run from the central chromatin mass to the nuclear “membrane” are continuations of the connecting filaments, but the part within the nuclear membrane is usually more distinctly visible than that without, probably because more thickly coated with staining matter. We see very clearly from these figures that the connecting

¹ These nuclear phases have already been recorded as vital phenomena. Hertwig has recorded them in *Actinosphaerium*, the contracted phase being found in starving forms (‘*Abh. k. Bay. Akad. Wiss.*,’ xix, 3 [1898], p. 637); and de Nabias noticed contraction of the chromatin in *Gastropods* on the application of chloroform (see ‘*Trav. Station Zool. Arcachon*,’ 1899, p. 36). The nuclear phases in the retina will be discussed later on (see below, p. 347).

filaments are continuations of the threads of the intra-nuclear reticulum.

These facts and illustrations—and the latter could be multiplied indefinitely—show that the nuclei of the middle layer are connected together not only *inter se*, but that filaments run from the nuclei that border the layer into the two reticular layers, proximally towards the ganglionic nuclei (figs. 15, 17 *c*, and 18 *d*) and distally towards the rod-nuclei (figs. 18 *a*, *b*, *d*, and 19).

Evidence for the Existence of Internuclear Filaments between the Nuclei of the Outer Nuclear Layer (the Rod-nuclei).

In the Amphibia this layer is thin, for the rods are stout, i.e. very nearly as thick as the nuclei. These nuclei, in crowding outwards, are often tightly packed, and hardly form a double layer. Junctions between them *inter se* are frequently obscured by the coarse masses of intra-nuclear chromatin which characterise the rod-nuclei of all retinas (see below, p. 338); figs. 18 *b* and *d* show, however, that they do exist. The connecting filaments are sometimes seen bridging intervals; at others the disposition of the chromatin within the nuclei shows that their networks are joined together. Further, the same figures show the nuclei of this layer connected with the nuclei of the middle layer, through the outer reticular layer. In figs. 18 *b* and 19 we have nuclei within or passing through the outer reticular layer on their passage outwards to become rod-nuclei, and these give off filaments towards the nuclei of both middle and outer layers. In fig. 19 the connecting filaments could not be traced through the cytoplasmic strands of the outer reticular layer; they were lost to view, just as they usually are within the cytoplasmic masses which, in the Mammalia, envelop so many of the ganglionic nuclei. But, in figs. 18 *a*, *b*, *d*, the filaments, being coated with staining matter, can be easily traced through this same layer. The dark stellate body in the

centre of fig. 18 *b* is not a nucleus; it will be referred to later on in this paper (see p. 339).

Figs. 20 *c*, *e*, *f*, are from the outer nuclear layers of different retinas, *c* of a thirteen-year-old cat, *e* and *f* of two different mice. As is usual in the higher vertebrates, the rods are very thin, and their nuclei have thus to be disposed in many rows. The filaments joining together the rod-nuclei in well-fixed retinas are frequently for some reason very conspicuous. The figures show the nuclei in different phases: in *e* the filaments radiate directly from a nearly homogeneously stained nuclear mass; in *c* and *f* there is a membrane surrounding the centrally placed chromatin. Similar figures could be given from other retinas (see, for instance, fig. 27 *d*).

The stellate character of the rod-nuclei has already been noted and figured by Gustav Mann¹ in the eyes of rabbits, but, being on another quest, he apparently did not follow the matter up and discover that the rays of adjacent nuclei meet and form connecting filaments.

Evidence for the Existence of the Internuclear Filaments between the Nuclei of the Inner Nuclear or "Ganglionic Cell" Layer; and again between these and the Nuclei of the Middle Layer.

The junctions between the nuclei in this layer show the same variations in visibility. At times no traces are to be seen; they are either ruptured or obscured by the tangle of the syncytial reticulum. In other slides, however, they come to view in a way which makes it astonishing that they have not been seen before. Figs. 8 and 12 are two drawings that might be multiplied indefinitely. Not only are the filaments themselves visible almost under a dry lens, but their connection with the intra-nuclear network of these large vesicular nuclei is especially clear. Other details shown in these figures will be referred to lower down.

¹ 'Journ. Anat. and Phys.,' xxix (1895), p. 100.

Further, the passage of the filaments from these ganglionic nuclei through the thick inner reticular layer to join the nuclei of the middle layer can be demonstrated. This is interesting for our future argument, for it shows that, in spite of the extreme delicacy of the filaments, they can persist over considerable distances, establishing organic connection between nuclei or systems of nuclei which are far apart.

It surprised me somewhat at first to find such delicate filaments running through a layer so variable in its texture. For, as we saw in Part V, the variations in the conditions of this layer are very great. Its strands are close and finely matted, forming a "punkt-substanz" in very young eyes, but usually become very coarse and irregularly meshed in older eyes. We have seen one cause for this in that its component threads are sooner or later thickened by becoming the tracks along which the absorbed pigmentary matter from the rods streams through the retina (see Part V). At the outset it would seem hopeless to endeavour to trace the nuclear connecting fibrils through this matted layer, since they are but just visible in a clear field, and this is so far true that I have never succeeded in finding them in the coarser conditions of the layer. But traces of them are occasionally visible when the layer is fine-textured (a "punkt-substanz"), and these traces are quite sufficient to justify our assumption of their presence as permanent structural elements. Very thin lightly stained sections will sometimes show a fine regular radial striation of the punkt-substanz. I have endeavoured to reproduce an instance in fig. 15. But the drawing is far too coarse. I had often before noticed such a striation crossing the usual tangential stratification of the layer at right angles, but had never understood it. Its real cause is, however, clearly shown in this figure, because it happened to be associated with nuclei of the middle layer which had their connecting filaments running into the reticular layer parallel with one another and evidently continuous with a certain number of the striæ.

When the layer is coarse-meshed, we must assume that the filaments bend about in the walls of the meshes. We are at

any rate bound to assume that the filaments find their way through, because nuclear filaments certainly plunge into the inner reticular layer from both sides (cf. figs. 14, 15, 17 *c*, and 18 *d*, with figs. 6, 7, 8, 10, 11). Since those which leave the nuclei laterally on each side run directly into adjacent nuclei, there can hardly be a doubt that those which plunge into the inner reticular layer on the one side are on their way to meet those entering the layer from the other side.

Reviewing the foregoing paragraphs, we see not only that the nuclei of the different nuclear layers are joined together inter se, but that the connecting filaments pass through the intervening reticular layers which separate the retinal nuclei into zones, so that all the nuclei of the retina are connected together into an organic system. I say an organic system because the evidence shows that the connecting threads are continuations of those which form the basis of the intra-nuclear reticulum. They are not mere suspensory fibrils, for which I first mistook them, but true extensions of the nuclear framework.

Summary of the Cytological Results so far obtained.

The retina, then, reveals to us a continuous nuclear system underlying its whole structure as a reticulum, whose filaments are achromatic and so fine as to be visible only with the best optical appliances, and then only when they are not obscured by cytoplasmic elements;—the syncytial framework and the masses of granular cytoplasm which envelop some of the nuclei. Their presence may, however, be revealed at any time during phases of physiological activity when they are coated with other substances. This “protomitotic” reticulum is so distributed throughout the retina that the nuclei which are themselves reticular are its nodes. All the other constituents of the retina, the various forms of cytoplasm outside the nuclei, and even the varied substances within the nuclei, have to be regarded in their relations to this underlying protomitotic system.

Without attempting in this place to review the many observations of others which tend either, on the one hand, to confirm, or, on the other, to make the existence of this system hard to accept, I will content myself with pointing out that it enables us off-hand to co-ordinate a long series of observations, some of which are now universally accepted, and to unite them for the first time into a connected whole.

In the first place, it directly confirms that doctrine of the essential structure of protoplasm which regards it as a mitomic framework (Flemming's "Fadengerüst") with "paramitomic" intervening substances (Flemming's "Interfilar-substanz," the hyaloplasma of Leydig as opposed to the spongioplasma). At the same time it tends to show that this analysis was incomplete. For the mitomic or proto-mitomic framework as now revealed is seen to be continuous, not only from cell to cell, giving thereby a new meaning to the intercellular bridges which have been recorded often enough to justify their claim to be of fundamental importance, but even underlying the nuclei. That an achromatic (linin) reticulum formed the basis of the nucleus has long been known, and a long series of observers have seen the threads of this reticulum extending beyond the nuclei, but their observations have not yet gained universal credence; indeed, nearly all recent cytological work seems to have been of a kind that failed to make the nuclear connecting filaments apparent. My own personal experience above described will show how easily that could happen. Nevertheless they exist, and the nuclei now stand in visible structural relationship with the rest of the protoplasm.

The best known doctrine that appeared to offer a co-ordination of these hitherto disconnected facts, the linin underlying the nucleus, the fibrillar structure of protoplasm, and the intercellular bridges, is that of Heitzmann.¹ But this doctrine will now require some modification, at least of interpretation. The dictum that every cell is a "prickle cell" and every nucleus a "prickle nucleus" is confirmed,

¹ 'Mikroskopische Morphologie,' 1883.

but we gather from the retina, in which the majority of nuclei have no granular cytoplasm, that the nuclear prickles run directly from nucleus to nucleus; whereas, on Heitzmann's system, each nucleus is connected by its prickles with a surrounding mass of cytoplasm, and each of these surrounding masses of cytoplasm is connected by its prickles with those that are adjacent to it. It is clear that a protomitomic system such as we have described, in which all the nuclei are joined by connecting filaments which would run through any cytoplasm associated with the nuclei and themselves form the basis of the intercellular bridges, would fulfil all the essential requirements of Heitzmann's description of the finer structure of protoplasm.

And here I would call attention to the fact that, according to Professor Macfarlane, in the case of plants also nearly all the separate elements for the demonstration of similar fibrillar continuity underlying the protoplasm are at hand. Professor Macfarlane¹ has recently emphasised them and indicated the direction in which they all point. All that is now required is the actual demonstration that the phenomena are all parts of one and the same system. This linking together of the chain cannot be long in forthcoming, since it has now been definitely accomplished for animal tissues, i. e. for the retina in the first instance. That it is a universal phenomenon we shall proceed to show.

But we have by no means exhausted the evidence to be gathered from the retina for the existence of this protomitomic system, nor have we attempted to correlate it with any of the known functions of the retina in order to see whether any light can be obtained as to its physiological importance.

We naturally proceed, then, to see if it is possible to make out the connections of the protomitomic system proximally with the nerves and distally with the rods. It is obvious that, if such a direct connection exist, we have the link, so long looked for in vain, between the nerve-strands, on the one

¹ 'Contributions from the Botanical Laboratory of Pennsylvania University,' vol. ii, Part II (1901), p. 187.

hand, and the rods in which we have every reason to believe that the nerves terminate, on the other.

As mentioned in the introductory remarks, all attempts to bridge over this intervening space by direct continuations of the nerve-fibres have hitherto failed. After their supposed union with the cytoplasm of the "ganglionic cells" they were lost, appearing again, as Max Schultze suggested, in the rod- and cone-fibres, which were, he thought, bundles of primitive nerve-fibrils, such as those found composing the axis-cylinders of medullated nerves. From here he at one time thought they ran outwards down the rods as striæ. We shall see lower down how near these suggestions came to the truth. At the time, however, they were not acceptable, because there still remained the gap between the ganglionic cells and these supposed bundles of nerve-fibrillæ, the rod-fibres. The discovery of the protomitotic system pervading the whole retina has put the problem on a new footing. The gaps that now remain to be bridged are those between the protomitotic system and the nerves, on the one hand, and the same protomitotic system and the rods, on the other.

The method of union between the nuclear or protomitotic system and the nerves was first discovered in the young stickleback, and once seen, was soon found in other retinas as well, and especially clearly in the preparations of the human retina to which I have already referred (Part V, p. 54). In the stickleback, a nerve-strand was noticed cut transversely (see fig. 6) showing the familiar characters, a number of darkly stained points which represented the individual primitive nerve-fibrils scattered on the walls of a delicate framework, and easily seen to be filamentous by focussing up and down. The delicate framework of the strand in such sections can only be regarded as supporting tissue conducting and isolating the fibrils.¹ A "ganglionic"

¹ This, I found, was the general structure of the nerve-strands of the Arachnida (see "Comparative Morphology of the Galeodidæ," *Trans. Linn. Soc.*, vol. vi [1896], p. 345). I have seen the retinal strands described as medullated, but that is not the case in any retina I have yet examined.

nucleus, just below the nerve at this spot, and having no associated cytoplasm, had its nuclear connecting fibrils perfectly preserved and quite clear and distinct, and each one ran into a separate fibril of the nerve-strand. Other instances were seen immediately after, and the figures might have been multiplied indefinitely. The nerve-fibrils within the supporting tissue of the strand were stained darkly and were comparatively thick, but the fibrils connecting them with the nuclei appeared colourless and of the same delicacy as those described above running from nucleus to nucleus.

On turning to sections of other eyes, especially those taken from the human retina, similar connections between the nerves and the nuclei were found in great multitudes, although, often as I had looked at the slides, I had never seen them before. I found them equally clearly in the sections in which the nerve-strands were cut lengthwise, as in those in which they were cut across. Though the individual nerve-fibrils were not by any means so sharply defined as in the stickleback, it was quite easy, in both cases, to make out the continuity of the nuclear filaments with the nerve-fibrils, as shown in the figures (7, 8, 9, 11, and 12). These figures are instructive, because they show not only cases in which the nuclei were quite devoid of all associated cytoplasm, but also others in which there were masses of this substance. In these latter, the nuclear fibrils showed the typical delicacy where they ran between the nerve-strand and the granular cytoplasm, but within this cytoplasm they would hardly have been visible, except for the fact that they are frequently beaded with minute staining clumps to all appearance exactly like those seen on the threads running down the rods (see fig. 21, and Part II, fig. 29 *b*).

These observations, connecting primitive nerve-fibrillæ with nuclei, are not by any means the first of their kind. Plüger¹ described in 1871 the nerve-fibrillæ running to the level of the nuclei of the cells forming the ducts of the

¹ Stricker's 'Lehre von den Geweben,' vol. i (1871), p. 312, figs. 76 and 80.

salivary glands; Arnold¹ and others claimed to have seen nerve-fibrils ending in the chromatin granules suspended on the intra-nuclear networks in unstriped muscle-cells, while a whole host of workers discovered connections between threads coming from the nucleoli of sympathetic ganglion-cells and their nerves.² I attribute the fact that these have never been confirmed, in spite of the special searches which have been made for them, mainly, judging from my own experience, to the accidents of fixation, but also to the discredit cast on them by the improbable nature of other phenomena described at the same time; these latter, however, as I shall show elsewhere, need not at all involve the existence of the filaments. Lastly, Haycraft³ described nerves ending in the nuclei of epithelial cells in the tortoise.

I mention these in passing to show that the claim that the nerve-fibrils are in organic connection with the intra-nuclear network is not new. No one, however, has hitherto been able to establish it; even the same worker has at times failed to confirm his earlier observations; the reasons for this the opening pages of this paper should make clear. There can, I think, be little doubt but that, had Max Schultze lived,⁴ the confirmation would have been forthcoming,—that is, if we may judge from his method of describing the fine structure of the nerve-fibres in Stricker's '*Lehre von den Geweben*' in 1871. After having written that, he could never have rested until he had discovered what became of the primitive nerve-fibrillæ which compose the axis-cylinder after they had entered the cell.

The discovery of the protomitotic system answers the question. The primitive nerve-fibrillæ of the retinal nerve-strands are continuous with the filaments of the retinal protomitotic system.

¹ Stricker's '*Lehre von den Geweben*,' vol. i (1871), p. 142, fig. 33.

² For a historical review, see, for example, '*Anatomie des Nervensystems*,' ii (1876), p. 130, by Key and Retzius, who themselves failed to find any continuations of the intra-nuclear reticulum beyond the nuclear membrane.

³ '*Quarterly Journal of Microscopical Science*,' vol. xxxi (1890), p. 563.

⁴ He died in 1874, at the early age of 49.

Having found, then, that the filaments of the retinal protomitotic system are proximally continuations of the nerve-fibrils, we have now to ascertain how, distally, this system is associated with the rods.

In Part II (page 447) I noted that Max Schultze, who was one of the first to discover threads or parts of them running down the rods, had clearly desired to regard them as the nerves. He reluctantly felt obliged to abandon that view because the threads seemed to lose themselves in the "connective tissue" of the outer layers of the retina. We are now in a position to clear up this difficulty. There can be no doubt that Max Schultze saw our nuclear filaments striating the inner limb of the rod. But he failed to trace them back into the intra-nuclear network of the rod-nucleus. Such an origin one would have thought must have been actually suggested to him by the observations connecting nerves and nuclei above referred to, especially as this would have served to link the striæ on the rods with the rod- and cone-fibres, in which he thought he saw, and in some instances I believe correctly, bundles of primitive nerve-fibrillæ. But, in his endeavour actually to see whence the striæ came, he was led astray by certain root-like streaks where the rods join the retina, and which often look like fibrils, but are, in reality, the streams of pigmentary matter absorbed by the rods and finding their way round their bases into the syncytial reticulum of the retina. This is evident from his statement that the fibrils run into the connective tissue; for here they join together to form the "Müller's fibres" (cf. Part V, Pl. V, figs. 25 *a-c*).¹ While admitting that it might be difficult to find any single preparation showing the whole of the details at a glance, it is none the less clear, from the facts described in these studies, that we must distinguish between these two systems of striæ. On the one hand, as we shall presently show, we have nuclear fibrils which are nothing less than the

¹ Borysiekewitz was also led astray by these, and concluded that the Müller's fibres must convey the nerves; see my remarks on this theory in Part V, p. 66.

distal fringe of the filaments of the protomitotic system, streaming from the rod-nuclei on to and into the rods; and, on the other, we have quite irregular streaks of matter finding its way out of the rods and along the syncytial framework as described and figured in Part V.

The connection between the striæ of the rod and the reticulum of the rod-nucleus is shown in figs. 18 *d* and 21, selected from many others. A rod-nucleus is shown in the former figure connected by filaments proximally with the nucleus behind it, while, distally, its own filaments are collected into a bundle which is limited by the outline of the rod. The same might also have been gathered from what has been described of rod-formation in Parts I, II, and IV. We saw there that each rod was a protrusion from the retinal syncytium of a vesicle which forced back the pigment cells—each vesicle being apparently dominated by a single nucleus. Threads descended from the nucleus on to and into the rod-vesicle with clumps of staining matter upon them, and were hence often referred to as staining threads.¹ Although, in these earlier papers, no special stress was laid upon the fact that these threads came from the nucleus, it was quite clearly stated, and figures were given to show that this was the case; for instance, Part II, fig. 29, and page 454.

The fig. 21 *a*, from the human retina, was selected because the peculiar and probably accidental arrangement of the chromatin masses within one of the nuclei made the connection specially clear. Faint suggestions of symmetry in the arrangement of the chromatin masses had frequently attracted my attention; I find in my notes figures of rod-nuclei with the chromatin arranged in approximate meridians; others in

¹ The expression "staining thread" was meant to describe the appearance shown in these figures. But we now know that this description is not really correct. It is true that the threads which form the longitudinal striæ down the rods are best seen when rendered visible by being coated with deeply stained matter, but at times, e. g. when inner and outer limbs of the rods have been partly pulled asunder, or when the staining matter is collected into disconnected clots, short stretches of the threads themselves become visible, but, being quite hyaline, are extremely difficult to see.

which the meridians had a spiral twist. For a long time I dismissed them as purely accidental phenomena, but now correlate them with the protomitotic filaments, as these latter run outwards towards the rods.

Figures showing the same connections between the striæ and the nuclei might have been given also from other mammals, e. g. from the rat. But these thin mammalian rods seem to have nothing like the number of fibrils running down their outer limbs as can be seen on the thick rods of the Amphibia (see Part II, Pls. 30 and 31), and their internal axial reticulum is greatly reduced.¹

We thus have the outermost fringe of the retinal protomitotic system running down the rods which are the end organs of the retina as an organ of vision, while the proximal fringe of the same system is continuous with the nerve-fibrils. We are now able to give a diagram (fig. 22) showing the protomitotic system forming the bridge between the rods and the nerves for the conduct of the stimuli.

The diagram is not intended to represent the true conditions, but only to illustrate the essential relations of the parts. The nuclei, for instance, are drawn too far apart; in very young eyes they may be tightly packed together (cf. fig. 14), and, in most eyes, they remain fairly crowded except in the innermost layer, which thins out first; the middle layer thins out only in very old eyes. On the right the two phases of the nuclei, which will be discussed below, are indicated. The syncytial strands other than those in the reticular layers are not shown, nor is any attempt made to indicate the very variable distribution of the granular cytoplasm.

¹ The internal reticulum, reduced in very thin rods to little more than a branching axial thread, has been seen and photographed by Dr. Lindsay Johnson, who claimed it as an axial nerve. This claim is apparently nearer the truth than was the axial nerve or nerves of Ritter and Hensen (see Part II, p. 450). I have, however, seen nothing that even appears to confirm Dr. Lindsay Johnson's claim that these fibrils are continued beyond the rod (see 'Arch. Ophthal.,' New York [1896], p. 450, fig. 26).

The diagram leaves one interesting point undecided. In some retinas, e. g. of man, it appears as if the fibrils from the rods run back as distinct rod-fibres into the middle layer (see the asterisk in the diagram), whereas, in other eyes (see fig. 20 *e*), no such isolated bundles appear to run through the layer of rod-nuclei, but the nuclei are all connected together into a network. Evidently both conditions occur. It is also fairly clear that all rod-fibres are not nervous. Two very important constituents of such fibres have already been described in Part V, viz. the strands of the syncytial framework and the pigmentary matter. Evidence that the nerve or protomitotic fibrils also take part in their formation, as was suggested by Max Schultze, will be given lower down.

From the vantage ground of this discovery of the protomitotic system, which we have now shown, not only morphologically but physiologically, to be of fundamental importance in the retina as a protoplasmic structure, several vistas of inquiry are opened out. It is perplexing to have to decide which to follow. The prominent position into which the doctrine of nerve discontinuity has sprung naturally tempts to criticism from the new point of view. This course, however, began to lead me into a treatise on the morphology of the nervous system, and threatened to extend this paper into a book. I had to decide to deal with it separately in an article to be published elsewhere.

Then, again, the "protomitotic system" may be expected to throw fresh light upon several burning questions in cytology. But here also a special treatise would be required.

The simplest and most useful plan will be to confine myself in this paper to the retina, and to give an account of the observations which I have been able to make as to the relations between the protomitotic system and some other of the retinal structural elements. It is by such observations alone that we can supplement what we know of the morphology of the protomitotic system by some insight into its physiology.

Observations on some of the Relations between the
Protomitotic System of the Retina and other
Constituents of that Organ.

The Cytoplasm.—There seem to be two distinct kinds of cytoplasm in the retina. There is the syncytial framework, consisting of hyaline strands and membranes, and there is the granular refractive substance found massed around certain of the nuclei in such varying quantities and indefinable shapes that no morphological value can be attributed to it. These two must be treated separately.

a. The Syncytial Framework.—The most obvious function of this is to serve as a support to the more delicate nuclear or protomitotic reticulum, although it is hardly likely that this is its only function. With regard to its origin, it is possible to regard it as having been built up of the ectoplasmic layers of what were originally a number of apparently discrete columnar "cells," out of which the retina has been developed; such cells still persist beyond the rim of the retina in what is known as the "*pars ciliaris retinae*." These "cells," lengthening and crowding together in layers, become spindle-shaped. The processes of change may still be seen in the rims of young amphibian retinas (see Part III, p. 33), and may be understood from the diagram fig. 24.

I described in Part III how at least the most characteristic portions of the present syncytial framework of the retina, viz. the zonal arrangement of its two reticular layers, may have arisen from the gradual rearrangement of the cytoplasmic strands of these spindle-shaped "cells." It is obvious that such a migration of the nuclei as was described in Part III would necessarily and effectually obliterate all traces of the separate "cells," and it seems only natural to regard the strands and membranes of the resulting syncytium as directly derived from the more stable outer (ectoplasmic) layers of the original "cells." They are clear and glassy, and show no likeness to the granular cytoplasm already noted as occasionally massed round the nuclei. As some confirma-

tion for this persistence of the ectoplasm, I may note that the delicate membranous walls of the rods can now and then actually be seen to develop from the radial cytoplasmic attachments of the spindle-shaped cells above mentioned found at the rim of the retina (see figs. 23 and 24). Even though we have no direct evidence, it is a natural assumption that these attachments are parts of the walls of the original columnar cells, and therefore ectoplasmic.

If this be so—that is, if the retinal framework is actually composed of the more resistant outer layers (ectoplasm) of the original row of single columnar cells which persists in the *pars ciliaris retinæ*,—then, whenever a chamber of the retinal ectoplasmic framework containing a nucleus also fills with granular cytoplasm, there results a kind of secondary “cell” formation. At any rate, it is quite possible that the question as to what is a “cell” and what is a syncytium may ultimately turn upon the arrangement of the hyaline ectoplasmic substance.

The syncytial framework, though much more stable than the granular cytoplasm, is nevertheless subject to great modifications; it is sometimes abundant, at others very scarce. And here, in passing, we may note a second function performed by the syncytial framework. In addition to being a support, its strands and membranes form paths along which streams of pigmentary matter, absorbed during the functional activity of the rods, escape through the retina. When these streams of matter are abundant and of old standing, they seem to effect a rearrangement of parts of the usually tangentially arranged syncytial strands, so as to form striking radial structures, the familiar Müller’s fibres (see Part V).

A variable unstable syncytial framework supporting a continuous protomitotic system presents no difficulty. It leads on naturally to the more stable frameworks which culminate in cartilage and bone. I may as well here call attention to the fact that, just as the protomitotic filaments must pass through the membranes of the retinal

framework (see fig. 13),¹ so must the protomitomic filaments of osseous and cartilaginous tissue pass through the interstitial substance characteristic of them, and the well-known canals receive in this way a new meaning.

But not only do the syncytial strands afford support merely as a kind of scaffolding for the protomitomic system; a much closer kind of relationship is also formed. For the nuclear filaments not only pass through the syncytial membranes; they may also run in or on the same. This is the case with the filaments in or on the walls of the rods, and with this we compare the running of the primitive nerve-fibrils on the supporting membranes of the retinal nerve-strands (see above, page 321). Again, when the strands of the inner reticular layer become matted and coarse-meshed, it seems as if the protomitomic filaments must run along them, as I have seen no sign of their passing through them.

b. The Granular Cytoplasm.—This is the refractive matter found massed irregularly around or on one side of the nuclei of the innermost layer and of some of the nuclei of the middle layer; the massing is always irregular, unless by filling a chamber of the retinal syncytium it receives from the latter a clear outline (see fig. 26). The same mass may sometimes envelop or be associated with two or three nuclei² (fig. 26 *m*, and fig. 2 *a*). It is most frequently seen on the distal side of the nucleus, and usually sends one or more tongues down into the inner reticular layer as if it were streaming away, which is especially the case when the tongues have no sharp outlines (cf. figs. 2 *a*, 3 *d*, 7, 9, and 12, with figs. 26 *a*–*e*, etc.). I regard these sharp outlines as due entirely to the syncytial framework. The dispersal of the cytoplasm

¹ In passing through a membrane of the syncytial reticulum, they are often bent at the point where they go through (see fig. 13). This bending may be due to post-mortem strains, and suggests an additional cause for the rupture of the filaments, if any other causes be required. For I am inclined to consider that the balling of the nuclei owing to the action of the fixing reagent is the chief reason for their disappearance from so many microscopic sections.

² This may be a possible explanation of Borysiekewitz's twin "ganglionic cells" (see 'Untersuchungen,' p. 19).

among the strands of the inner reticular layer may perhaps give rise to some of the "dendrites" of these "cells," such as are revealed by Golgi's method. The streams of pigmented matter such as I figured and described in Part V, are, however, I believe, the explanation of most of them. In neither case, whether as streams of cytoplasm or of pigmented matter, do they supply us with structures of any morphological value. The forms assumed are mere passing physiological phases, except, perhaps, in old eyes, in which the Müller's fibres may have acquired some stability (see Part V, Pl. 5, fig. 32 *a*).

All the appearances are as if the granular cytoplasm were purely nutritive and had only a passing association with the nuclei. The observations I have been able to make point in this direction. A number of salamanders accidentally neglected for nearly six months were found alive but emaciated. Not the faintest trace of the cytoplasm could be found associated with any of the nuclei of the innermost layer in any one of them. This observation, however, is not very conclusive, because very little indeed can be found in normally fed salamanders, or, indeed, in the Amphibia as a rule. My experience is that it is rare to find a nucleus actually enveloped in cytoplasm in this group, and that anything even approaching the typical diagrammatic ganglionic cell must be looked for among higher vertebrates; they seem to be most common in the higher mammals, especially in man. Hence it is of significance to note that in several sets of sections of the retinas of mice which had been tired out by long (three hours) exposure to the light of an arc lamp, every trace of granular cytoplasm had vanished, while, in other retinas from wild, albino, and other mice, which had not been put to this strain, most of the ganglionic nuclei had at least a tongue of this matter trailing off into the inner reticular layer, though very few were completely surrounded by it. Lastly, in the sections of the human retina to which we have frequently referred above, the majority of the nuclei of the innermost layer, at least near the yellow spot, are nearly, if not quite,

surrounded with cytoplasm. This eye had been bandaged and very little used before excision; hence, perhaps, an accumulation of this material. These observations point towards experimental confirmation of our inference that the granular cytoplasm is nutritive, and that, in its passage through the retina, it is seen in more or less accidental association with the nuclei. We shall see lower down, when describing the "Nissl's Schollen," that the evidence for the streaming of the cytoplasm distally is greatly strengthened.

In the middle layer, granular cytoplasm is only occasionally associated with the nuclei. In mammals in which, as is well known, the capillaries penetrate into this layer, it may surround a nucleus here and there, and even render a syncytial chamber turgid. It will be an instructive study to see if any close relation can be found between the capillaries and the distribution of this matter. In this middle layer, however, it is most frequently seen as a small tongue streaming inward into the inner reticular layer, the natural inference being that it is not streaming away, but arriving, having come through the inner reticular layer from the ganglionic nuclei from which, as we have seen, it appears to be streaming. The suggestion is that, as it emerges from the inner reticular layer, it attaches itself to the first nuclei of the middle layer which it reaches.

This mere transitory association between the granular cytoplasm and the nuclei in the retina is in strange contrast with what we see in most other tissues. In the typical cell the nucleus is always enveloped by what is to all appearance a discrete mass of cytoplasm. A nucleus without cytoplasm has hitherto been thought almost an impossibility, and, doubtless, for many tissues, e.g. in all epithelia, it is an impossibility, the reason why being not far to seek. Assuming for the present what can be easily proved, the existence of a special protomitotic system for each tissue, epithelia represent outer fringes of such systems, and it is inconceivable that the delicate protomitotic filaments themselves should project without some covering; even when they run out into the

finest cilia, they must be thought of as sheathed in cytoplasm.¹ No such difficulty exists in the way of what, for purposes of observation, we may call naked nuclei within the retina, for, as a matter of fact, they are not any more really naked than are the nuclei in many ordinary cells in which there is a perinuclear space. Indeed, as already pointed out, the chambers of the retinal syncytium may be regarded as perinuclear spaces with one or more nuclear nodes of the protomitomic reticulum suspended within them. And round these nuclei, and in close contact with them, an unstable, probably nutritive, granular cytoplasm occasionally accumulates.

One word in passing as to the bearing of this upon what is known as the cell theory. The inadequacy of this theory has long been felt, and has found expression at the hands of eminent biologists.² But the attack centres round the fact that the cell doctrine cannot be reconciled with certain phenomena, especially relating to development. The theory does not go deep enough. It has been framed, it is true, with reference to a large but yet limited number of phenomena; further research has been showing it to be superficial. The retina has now revealed a continuous fibrillar system (parts of which were already well known) underlying all protoplasmic structures. This system reduces the "cell" to its true position. It is no longer a mass of cytoplasm containing a nucleus, but a node of a protomitomic system with cytoplasmic matter massed round it. It has long been admitted that the essential of the cell is the nucleus, without which the protoplasm dies, and now we know that the nucleus is, in essence, a specially complicated node of the protomitomic system. This protomitomic system, with its nodes, is the deeper underlying factor in relation to which these masses of cytoplasm accumulated round the nodes; that is, the cells are

¹ The protomitomic system in general will be described elsewhere.

² See Professor Whitman, 'Wood's Hall Biological Lectures,' 1893; also Professor Sedgwick, 'Quart. Journ. Microscopical Science,' vol. xxxvii, 1894.

secondary phenomena. At fringes of these systems the cytoplasmic masses may be in more or less stable or apparently stable blocks, or columns, or plates, and form epithelia. In solid tissues, with great quantities of granular cytoplasm, this matter will be massed as so many balls, more or less uniform in size, round the nuclear nodes of the protomitomic system, each mass being as a rule distinguishable. The distribution of the cytoplasm is wholly secondary to, and always dependent on, the forms of the underlying protomitomic systems. And though the cell doctrine will still be of use in describing the method of distribution of the cytoplasm and its special constitution in any tissue or organism, it can be of no further service to us in profounder questions relating to the physical basis of life, such as those dealing with growth and development,—that is, indeed, in relation to those very subjects in which its failure has already been recognised.

Before quitting this subject I should like to call attention to fig. 26, in which I have selected, out of an immense number of drawings, a few of the cases which show the granular cytoplasm with nearly the same outline as the nucleus with which it is associated. I offer no explanation of this. It can hardly be a case of mere coincidence, or be due to the accidents of fixation; and even then, in the latter case, it would require explanation. The figures are taken from different retinas, which shows that the phenomenon may occur under certain unknown conditions at any time. It has, perhaps, helped to lead me to the conviction that the granular cytoplasm is attracted to the nuclei, as above suggested.

Some Observations on the Relations of the Chromatin to the Underlying Protomitomic System in the Retina.

Hitherto, the chromatin has had every claim to be regarded as by far the most important of the constituents of the cell. Its storage in a differentiated portion of the cell, the nucleus; its ascertained physiological importance in

vital phenomena; and lastly, its startling movements during cell division, have forced the more passive cytoplasm into the background. It has even been somewhat prematurely called "the hereditary" substance.

What the relations are in their entirety between this important substance and the protomitotic system remain still to be discovered, but we are able here to describe certain suggestive phenomena. The bare description of the structure of the latter system would have been sufficient to guarantee its fundamental importance for the proper understanding of organic life, did we not know at the same time that its threads are the paths along which the nerve-stimuli travel. Such a system clearly rivals the claim of the chromatin to the first place, and their mutual relations become a matter of supreme interest.

The most important result arrived at is that the chromatin, like the granular cytoplasm, is an unstable quantity in the retina, in that it also streams outward towards the rod-layer. Unlike the granular cytoplasm, which seems to travel freely among the strands of the syncytium (although the exact nature of the movements have still to be made out), the chromatin only travels along the protomitotic filaments. Its morphological value, therefore, like that of the cytoplasm, is small, depending solely upon the fact that it tends to accumulate within the nuclear nodes and in varying forms and quantities.

The evidence for the streaming of the chromatin from nucleus to nucleus is of two kinds, direct and indirect.

The direct evidence is not abundant, but, taken together with the indirect, it is very significant. As already described, the protomitotic filaments, as they run from nucleus to nucleus, are usually made visible when coated or beaded with staining matter. In young, developing rods, continuous streams of such matter can sometimes be seen (Part II, figs. 15 *a*, 27 *c* and *d*) ; at other times a string of beads (see Part II, figs. 3 *a*, 27 *b*). In fig. 18 *c* of this paper, the staining matter is irregularly clotted on the connecting filaments,

while in figs. 10, 11, it is again beaded on the filaments as they run through the cytoplasm. The evidence shows, then, that whereas one normally finds the chromatin massed in and confined to the nuclei, there are times when it is found travelling beyond the usual nuclear limits on to the connecting filaments. That the chromatin can leave the nucleus and wander into the cytoplasm surrounding it has long been a recognised fact. The discovery of the protomitotic filaments throws a new light upon this wandering. Whether there is any cytoplasm or not, the chromatin travels along the protomitotic filaments.

The most conclusive evidence that this chromatin, seen in clumps and beads upon the connecting filaments, is actually travelling from nucleus to nucleus outward, is gathered from a study of the whole retina.

In very young eyes, before they have commenced to function, the chromatin is fairly evenly distributed among all the nuclei alike, but sooner or later this condition changes, and the bulk of the chromatin is seen in the outermost nuclei. Fig. 25 is from a kitten two days old; it shows nearly all the proximal nuclei as clear, almost empty vesicles, but a most striking accumulation of the chromatin in the nuclei along the distal edge of the retina, i.e. in the rod-nuclei. I have no embryonic cats' eyes, but, judging from other embryos, we may assume that this accumulation of the chromatin is secondary. It is evidently preparatory to rod-formation.

The first great structural change in the retina after birth is the production of the rods as a compact mass of vesicles protruded from its distal surface. Into each of these rods a staining reticulum grows out from its nucleus, the distribution of which within the rod has already been described. A general migration of nuclei towards the place where new rods are to be protruded can be seen, a migration which reminds us of the movements of the nuclei in vegetable filaments towards the spots where growth is about to take place.¹

¹ See Haberlandt, 'Ueber die Beziehungen zwischen Function und Lage des Zellkerns,' Fischer, 1887.

Further, any healthy retina of any age, if properly fixed, will, as already described, show the filaments running down from the nuclei on to the rods coated or beaded with staining matter. So that we are justified in concluding that large quantities of chromatin are not only used up in the development of the rods in the first place, but continue to be used up in the life activities of the rods.¹ The immediate source of all this chromatin is the rod-nuclei.

Turning, then, to these rod-nuclei, we find that in spite of this immense and continuous drain—immense because, apart from the supply needed for its functional activity throughout life, each rod, in the course of its production, must require more than a single nucleus could contain,—in spite of this drain, these very rod-nuclei remain especially rich in refractive staining matter. This richness in chromatin of the rod-nuclei is one of the first facts that strikes a diligent student of the retina, no matter what eye is studied; although it is seldom so marked as shown in fig. 25 above quoted, it is always striking. In the other retinal nuclei the chromatin is fairly evenly distributed over the nuclear reticulum, with usually one, perhaps two, conspicuous masses (nucleoli);² but in the rod-nuclei it is invariably collected into large, sometimes immense clumps. These coarse clumps of chromatin are specially striking in those animals in which the rod-nuclei are long and spindle-shaped. Figs. 20 *b*, from the retina of a cat six weeks old, and 20 *c*, from that of a very old cat, show the kind of banded appearance which the nuclei acquire owing to the arrangement of these chromatin clumps in single rows within nuclei of that shape.

In the rabbit there are frequently two clumps with a single clear band. This appearance has frequently been noticed by earlier observers, and thought to have some peculiar physiological significance. It is, however, the

¹ See Gustav Mann, 'Journal Anat. Phys.,' xxix (1895), summary.

² The most conspicuous nucleolus is seen in those nuclei in which the chromatin is all balled together in the centre, here regarded as a phase (see p. 347).

simplest way of arranging large masses of chromatin in a long fusiform nucleus.¹ That this is the true explanation we learn from fig. 20 *a*, which represents a rod-nucleus of a kitten (two days old), that is, at an earlier developmental stage than that shown in fig. 20 *b*; while fig. 20 *d* shows a nucleus on its way from the middle layer to become a rod-nucleus with the chromatin in it commencing to form clumps.

Continuing our argument, the large supply of chromatin maintained in these nuclei, in spite of what they are passing on to the rods, must either be manufactured in situ or else come from without.

The latter is the more probable view, because of the extreme distal position of these rod-nuclei, viz. in the front line of functional activity and furthest from the centres of assimilation. But fortunately we need assume nothing, for figs. 18 *a-d* show the protomitotic filaments thickly clotted with staining substance, which we can safely assume to be travelling from the nuclei of the middle layer into the rod-nuclei.

In this connection I believe we can find the explanation of a very common phenomenon in the retina. Fig. 18 *a* shows two clumps of staining matter, one of which is very large, and fig. 18 *b* one clump, outside the nuclei, and clearly themselves not nuclei. In Part V, I called attention to certain clumps of matter in or on the outer reticular layer which are frequently seen in chambers formed by the ends of what are called the rod-fibres. The resemblance of these clumps within chambers to small nuclei in cells has, indeed, suggested to one observer (Borysiekewitz) the presence of a new row of "cells" in the retina (cf. fig. 18 *b*). The very large mass in fig. 18 *a* is on the horizontal threads of the outer reticular layer, but in fig. 18 *b* a mass is shown within a chamber of the retina. These, as stated, are certainly not nuclei; they are contained in no vesicles with sharp contours like the membranes of

¹ On this subject compare a discussion in vols. xv and xvi of the 'Anat. Anzeiger.' My own observations are not quite in accord with Dr. Schaper's, for in very young cats the rod-nuclei have distinct networks (see fig. 20 *a*).

nuclei. They are also not the clumps of pigmentary matter which sometimes terminate the rod-fibres, as shown in Part V, fig. 21, but they are the equivalents of the stellate bodies seen in chambers in the rod-fibres shown in fig. 20 *b* on the same plate in Part V. After a long and careful comparative study of these bodies, I feel fairly safe in affirming that they are large extra-nuclear masses of chromatin, attached as they should be by threads to the surrounding nuclei. The one figured on the right in fig. 18 *a* has been selected because it is the very largest I had ever seen in any retina. But almost any good section of a frog's retina will show a score or two of them all along the outer reticular layer. Owing to the thinness of the layer of rod-nuclei in the frog there are seldom any conspicuous rod-fibres, which are only really pronounced in animals in which the rod-nuclei are many layers deep. In these cases the rod-fibres, on reaching the outer reticular layer, end either in a knob or in a chamber-like expansion of the fibre. The knob is, I believe, as already stated, a mass of pigmentary matter arrested against the outer reticular layer, while the chamber is an expansion of the fibre, in some way due to the presence of one of these masses of extra-nuclear chromatin which takes up its position within it.

At the present moment these masses of extra-nuclear chromatin are interesting as evidence for the passage of this matter outwards. It looks as if, just as the pigmented matter, passing inward from the rod, is arrested on reaching the outer reticular layer, the chromatin also, passing outwards, may be arrested temporarily by the same layer. I have, for instance, frequently seen, in the human retina, a little plate of staining matter like that shown in the diagram fig. 22, where the fibre of the rod which is marked with an asterisk passes through the outer reticular layer; this plate is resolvable into minute granules.

Passing on, we have to ask—whence do the nuclei of the middle layer obtain their supply? Capillaries are only known to penetrate to this layer in the higher vertebrates. Hence we are driven to conclude that it must come through

the inner reticular layer from the "ganglionic" nuclei. I am inclined to look to what are known as "Nissl's Schollen" within the ganglionic cells for light on this subject. These "Schollen" may be regarded as consisting of dense crowds of minute masses of chromatin (microsomes), whose origin from the nuclei can easily be demonstrated under the microscope by noting not only their usually concentric arrangements round the nuclei (see fig. 26, especially *e*), but also the relative positions of and connections between the clots and the intranuclear masses (see figs. 1 and 26 *g*, *k*, and *m*). Further, retinas may be found in which deeply staining clots can be seen adhering closely to the sides of nuclei which have no granular cytoplasm at all (fig. 5), a fact which shows that this latter substance plays no direct part in their production, whatever influence its presence may have on their distribution and constitution as clouds of microsomes. Their origin from the nuclei is, indeed, generally admitted.

All the microscopic appearances suggest most unmistakably that these "Schollen" are streaming away into the inner reticular layer, together with the granular cytoplasm in which they are usually embedded. No one, indeed, can examine "cells" such as those I have attempted to figure (fig. 26) without coming to this conclusion; cf., for instance, the massing of the "Schollen" proximally, and their comparative scarcity distally; while those which do occur on the distal side are very frequently drawn out into the processes of the cells, down which they thin away to invisibility. These speak for themselves. Here, then, we have evidence that chromatin escapes from the ganglionic nuclei and makes its way with the granular cytoplasm through the inner reticular layer towards the middle layer. In this case, however, we do not exactly know whether, in moving outwards, it travels along the protomitotic filaments, or independently. The former supposition is the more probable, as we shall presently see. Meantime, what we can justly assume is that it finds its way into the more distal nuclei to replace the chromatin that streams away into the rod-nuclei and ultimately into the rods.

Having traced the outward movement of chromatin from the innermost layer of nuclei through the retina and ultimately into the rods, we come to the last question: is it formed in situ in this innermost "ganglionic" layer of nuclei, or derived from without? In this layer we find a rich blood-supply in all the higher vertebrates, while, in the Amphibia, vessels run close to it though they may not actually penetrate it. But whether the "ganglionic nuclei" receive chromatin from the blood circulation or not, I should like to venture on a somewhat daring suggestion in favour of at least part of it being derived from a source unconnected with these blood-vessels. My suggestion is based upon the following observations.

The minute staining clumps or beads upon the protomitotic threads which run down the rods receive their explanation from the fact that chromatin is travelling along their threads from the nuclei into the rods. Other phenomena confirm this conclusion. But we occasionally find similar staining clumps upon the filaments which connect the ganglionic nuclei with primitive nerve-fibrils (figs. 7 and 11). In fig. 11 these beads of staining matter are only seen on those portions of the fibrils which run within the cytoplasm, while the portions between the cytoplasm and the nerve-strand are the usual exquisitely delicate filaments devoid of any beads of staining matter. But these delicate filaments are in startling contrast with the primitive nerve-fibrils, which are comparatively thick and deeply stained, as shown in figs. 6, 7, 8, 9, 11. What is the meaning of the sudden contrast in thickness and colour? How comes it that the filamentous continuations into the nuclei of thick staining fibrils suddenly become exquisitely fine and perfectly hyaline? I cannot refrain from suggesting (1) that in life there is a stream of chromatin along each nerve-fibril; (2) that this stream would hardly be travelling from the nucleus, where, according to our previous argument, it is greatly needed; and (3) that the sudden action of the fixing reagent causes this stream to contract partly back into the

nerve-fibril on the one hand, and into the cytoplasm on the other, leaving the filament naked. This seems to me to be a possible interpretation of the microscopic appearances. I may add that we have already seen how the action of at least one fixative, e. g. boiling corrosive sublimate, leads to the displacement of chromatin along the connecting fibrils. This apparently occurs on a large scale in retinas so fixed; some have the nuclei balled together into compact globules of chromatin, others spread out into amœboid masses united by their processes into a network (see fig. 16). I propose to follow up this subject as to the possibility of a stream of chromatin passing along the nerve-fibrillæ, in another paper dealing specially with the nervous system, and must content myself here with making the suggestion as perhaps throwing light upon the origin of at least part of the chromatin which streams through the retina.

In addition to the different forms above described under which the chromatin seems to escape from the nuclei, viz. as beads, as continuous streams clotting the connecting filaments, and as crowds of microsomes forming the "Nissl's Schollen," there is another method occasionally seen which requires a good deal of further investigation.

Various sized, spherical, highly refractive masses, each in a small clear vacuole, are met with outside the nuclei. I have found them in the granular cytoplasm of the ganglionic nuclei (fig. 26 *a*) and in the rods (Part II, figs. 29 *c, d, f*). In both of these situations they have been seen by others. When seen in the former situation they have usually been called centrosomes, and a special physiological significance has been attached to them. In the rods, one was figured by Hensen years ago, but was apparently passed over without comment. There can, I think, be little doubt that these must also be regarded as so much chromatin escaping from the nuclei. In the first place, they bear such a striking resemblance to similar bodies frequently seen within nuclei. Both inside and outside of the nuclei, they are always surrounded by a clear ring representing a fluid envelope. Within the nuclei

the radiating fibrils attaching them to the rest of the intranuclear reticulum can be seen, perhaps because coated with staining matter, but outside the nuclei these fibrils are apparently too faint to be visible; at least, I have never seen them except when they have occurred in the rods, in which cases, again, their connecting threads are coated with staining matter (Part II, figs. 29 *c*, *d*, *f*; while fig. 15 *a* of the same part shows one flattened out against the membrane dividing the inner from the outer limb of the rod, and two streams of staining matter flowing from it, presumably along the filaments with which it was associated). Fig. 29 *c* (Part II) actually shows one of them upon a stained filament, along which we may assume that it travelled.

The origin of these "centrosomes" from nuclei seems to be fairly widely acknowledged, and also their connection with filaments. They occur in special numbers in ciliated epithelium, apparently only as another form of the chromatic basal bodies, to which we shall refer elsewhere.

There is evidence, then, that these refractive deeply staining globules are merely parts of the stream of chromatin passing outward through the retina. What else they may be we cannot yet say. The difference between them and other equally large, but less refractive and irregularly shaped beads without clear vacuoles, may be due to slight variations of physiological or chemical condition.

While speaking of large masses of chromatin leaving the nuclei as masses, I may call attention to a curious phenomenon found in the retina of the mouse and in some other vertebrates. In all my preparations of mice, one or more very large clumps are seen adhering to the walls of the nuclei—indeed, not infrequently protruding and standing out on the outer surface of the nuclear membrane as sharply projecting knobs. I have, however, never found any of them away from the walls on any of the connecting filaments. I first noticed them before I had discovered the general movement of chromatin from nucleus to nucleus, and was naturally greatly struck by this extra-nuclear chromatin, as was also my friend the late Mr.

Martin Woodward, to whom I showed it. I now naturally connect the phenomenon with the streaming process, but exactly how I do not yet know. There does not appear to be any clear envelope of fluid round them as there is round the refractive globules above mentioned, even though they may be much larger in size. Another difference to be noted is that the refractive globules are always perfectly smooth and usually spherical, whereas these are not. They are probably comparable with the extra-nuclear masses described above, pages 338 and 339, and shown in figs. 18 *a* and *b*, which are also never surrounded by fluid envelopes or films.

We gather from the foregoing that the chromatin is a less stable constituent of the retina than the protomitotic system. On the other hand, we know that chromatin is necessary to the life of the cell. And so certainly is the protomitotic system, for I shall be able to show lower down that this system is not a mere passive framework, but that its filaments appear to take an active part in vital processes. We apparently, then, have at least two visible factors in protoplasm, both of which may be regarded as essential: the underlying, more or less stable protomitotic filaments, and the chromatin, the visible distribution of which shows it either stored in the nuclei or travelling along the aforesaid filaments; but what the character of the association between them is has to be discovered. This is but another form of the old problem of the relationship and the relative importance of the nucleus and the astral body, the former representing the chromatin and the latter the protomitotic system.

On the Movement of Fluid through the Retina,
and on some Phases of the Nuclei probably
correlated with this Movement.

Parallel and probably intimately associated with the stream of chromatin just described as passing outward through the retina, there is a steady flow of fluid. The chromatin travelled, as we saw, along the fibrils of the protomitotic

system; the movements of the fluid cannot be so accurately defined. There is evidence, however, to show that it is associated with the nuclei. Indeed, certain phases passed through by the nuclei seem explicable only on this assumption.

The first evidence for the existence of this stream is seen in the early stages of rod-formation. The rods begin as vesicles of fluid protruded from the retina. Some of the processes have been described in Parts I, II, IV. A compact mass of delicately walled vesicles push back the pigmented epithelium, and each eventually becomes a cylindrical rod filled with other substances besides fluid. In every case in which we have analysed the successive stages in rod-formation, whether in young eyes when the rods are short oblong vesicles, or in older eyes when each new rod has to pass through a long slender cone phase, we found that they seemed to pass in turn through certain definite changes of shape. These different form-phases could be best explained by a periodicity in the discharge of fluid into them; each protrusion not only altered the shape of the particular rod, but, in so doing, compelled a change of shape in those around it.¹

Further, there is microscopic evidence for such discharges. In the Amphibia, we not only see the large vacuolar basal ends of some cones contrasting strongly with others with thin and more solid-looking bases, but we have a corresponding contrast in the appearances of their nuclei. These, at least in the earlier stages of rod-formation, show two very distinct phases—one large, clear, and vesicular, the other small and full of chromatin (cf. the figures, Part II, fig. 23, contrast the two elements on the right of the figure).

When the rod has reached its normal size, the large periodic discharges which seem necessary to protrude the rod are apparently no longer required. The rod-nucleus appears to remain fairly uniform in size, but nevertheless keeps up a more regular smaller discharge of fluid into its

¹ Except when discharged among fully formed rods which undergo no further changes of shape.

rod as one of its normal functional activities. In Part II, fig. 17, this discharge of small globules of fluid into the rods can be seen; the same also can be seen in the newt, Part II, fig. 30. In both cases the fluid clearly comes from the nuclei. In all the mammalian eyes I have examined, the existence of globules of clear fluid can be seen in the rods. I am further inclined to regard the large inner limbs of a certain number of the rods in the human retina, which, on that account, have been called cones and considered as of special morphological value, as simply due to the fact that they have just received, or are in the act of receiving, a discharge of fluid. In all essentials they are ordinary rods, and, so far as appearance goes, differ in no other respect than that their inner limbs are swollen up with fluid. The mammalian cone is thus apparently simply a normal physiological phase in the life of the rod. All the rods of the human retina probably pass, every now and then, through a cone phase, most rapidly and frequently where functional activity is greatest, i. e. in the region of the fovea centralis, where the rods are of increased length.¹

Further evidence for the origin of this fluid from the nuclei may sometimes be seen at the rim of the retina in young tadpoles where rod-formation is beginning. Fig. 24 shows a most instructive series, frequently but not always seen. The large columnar cells inside the iris contain distally a great fluid space, the nucleus, with some cytoplasm, being confined to the proximal end of the cell. The chromatin network invades this fluid space at one end, and pigment granules at the other. This is, in brief, the description which can be given of the rods, except that the latter protrude beyond the membrana limitans externa. Where the iris passes into the retina the cells become transformed,

¹ As shown in earlier papers, the cones are not homologous or even analogous structures in different eyes. The cones of the Amphibia are young rods; the cones in the fish have an entirely different significance (see Part V), while the cones in the human retina admit of the simpler explanation given above in the text.

and, losing the long cylindrical shape, pass into the many-layered spindle-shaped nuclei attached by radially arranged cytoplasmic strands to the two limiting membranes of the retina. Here, again, we may find fluid vesicles at the distal ends of some of these cytoplasmic strands (figs. 23 *a, b, c*), which, as we move in towards the centre of the retina, protrude further and further beyond the external limiting membrane, as the first beginnings of rods. Again, individual nuclei well within the retina may even be here and there seen with a vesicular excrescence, into which the nuclear reticulum sends out radiating filaments (fig. 23 *b*). These phenomena speak for themselves. They link on perfectly naturally with the different stages of rod-formation already described in former parts. I am especially tempted to call attention to the analogy between these long cytoplasmic strands with their terminal vesicles and the long thin cones which swell into vesicles after passing through the rod-layer. The point which at present claims our attention, however, is the fact that the fluid which causes these vesicles and eventually swells them into rods can, so far as microscopical appearances go, only have come from their respective nuclei.

We come once more to the question—whence do the rod-nuclei receive their supply? A comparison between the sizes of the rods and the sizes of the nuclei shows that no nucleus could protrude a rod from its own fluid contents. In order to fill a rod it must pass on fluid which it receives from elsewhere. And this brings us to a phenomenon which, so far as I can explain it, points to a systematic pulsation of the retinal nuclei, a pulsation which sends the fluid through the retina outwards and into the rods.

Let us take first the microscopic appearances which suggest the existence of pulse waves through the retina. The first is the fact that, in every well-preserved retina, in addition to the nuclei which may be considered normal, are others in great numbers in two opposite phases. On the one hand, we have large vesicular nuclei with scattered chromatin, and, on the other, either small round nuclei with compact chro-

matin, or else nuclei in which the chromatin has contracted to a dense refractive mass in its centre.

Such stages are very marked in the "ganglionic" layer, for here the vesicular nuclei attain sizes reached in no other layer. The contrasts between the phases in this layer are sometimes very great (see figs. 2 *c*, and 3 *a*, *b*). I have measured many hundreds of these contrasting nuclei in this layer, and have found them range between as much as 18 μ and 4 μ . The contracted nuclei are frequently associated with fluid spaces in the inner reticular layer, as if fluid had just been discharged from them. I was, indeed, at one time inclined to think that this propulsion of fluid was one of the chief functions of the nuclei of this layer. But I soon noticed that these phases were to be met with through all the layers of the retina.

Further, it is to be noted that these phases of the nuclei are sometimes found in zones. These zones are naturally most marked in the middle layer, because in that there are most nuclei. In this layer almost every observer has noted that the innermost of its nuclei are usually large and vesicular, while the outer are smaller, and with denser chromatin. These zones are, however, not homogeneous, for among the vesicular nuclei others which are contracted can always be found, while, among the contracted, others in the vesicular stage occur. But it is not only in the middle layer that this is marked. Figs. 22 *b*, *c*, Part V, show parts of the section of a plaice in which the nuclei of all the layers show zonal arrangement. In the two inner layers, the vesicular nuclei are again on the proximal side, but, in the layer of rod-nuclei, a line of vesicular nuclei runs along the middle of the layer, with contracted nuclei on both its inner and outer sides. Except in this outermost layer the zones are not sharply marked off, but there is a good deal of mixing. It is difficult to account for such a regular zonal arrangement of the two kinds of nuclei (vesicular and contracted), except on the assumption of a series of waves of pulsation passing through the retina, the phases of which are fixed in the preparation.

It may be noted in passing that the expulsion of the nucleoplasm, and the consequent contraction or balling together of nuclei into compact masses of refractive chromatin, is not a new phenomenon,¹ but in this present case the contractions are spontaneous, and fulfil a distinct purpose.

It is worth while pointing out that there is ground for believing that the fluid is discharged from the nuclei with some force. It is only on such a supposition that we can explain many of the phenomena of rod-formation, such, for instance, as the forcing of the long cone through the whole layer of rods in its earliest stages (see Part I, figs. 2 *a*, *d*), the changes of shape, and the shifting of the contents of the young rods in certain stages, in consequence of another rod-vesicle being thrust in among them (see Part I, figs. 4 and 7, *c*₄ and *r*₁). Lastly, in retinas which are either embryonic or have not yet become functional, no rods being yet formed, the pigmented layer is in close contact with the external membrane of the retina. It is apparently only pushed away by the protrusion of the rod-vesicles. This, again, implies some force, especially when we remember the tendency of the pigmented cells to push towards the light.

An objection, however, may be raised against this suggestion of pulsations, or at least against the suggestion that these pulsations pass through the retina in waves, as an explanation of the zonal arrangement of the two nuclear phases.

It may be asked why, if this zonal arrangement represents a series of pulse waves, the zones do not alter their relative positions in different retinas? Why is it that, in all eyes, the vesicular are always on the inner side, and the contracted on the outer side of the inner and middle nuclear layers? If there were waves, some preparation ought to show these waves in other positions. The explanation of this I take to be as follows:—The source of the fluid is probably the blood-vessels on the inner or proximal side of the retina. Hence the

¹ Dr. de Nabias has seen it in Pulmonate Gastropods; see 'Trav. Station Zool. Arcachon,' Année 1899, pp. 36—38.

proximal nuclei might be expected to fill up fastest, and a difference in this small matter, viz. in the speed with which the nuclei again become vesicular, would be enough to account for the apparent fixity of the zones. A larger number will always be found in a condition to discharge in the inner than in the outer zones, in which the nuclei remain longer in the contracted condition.

Putting the evidence together, I think that there can be little doubt but that the outward stream of chromatin above described is accompanied by a stream of fluid, and that the active agents in causing the movement of the latter are the nuclei that swell and become vesicular, and then contract, either as wholes or by the chromatin network within them contracting and expelling the accumulated fluid. The existence of some close association between the fluid and the chromatin can be gathered from other facts as well, viz. from the normal structure of the nucleus itself, which is a turgid fluid vesicle and apparently a storehouse for chromatin, which latter substance is thus bathed in fluid; and also from the fact that the refractive chromatin masses, the so-called "centrosomes," are invariably accompanied by a shell of fluid. On the other hand, however, it is to be noted that no fluid seems to accompany the non-refractive chromatin which streams along the filaments, and even accumulates in clumps, e. g. in the outer reticular layer (see figs. 18 *a* and *b*).

It is possible that the above is not quite the right interpretation of the phenomena, but, speaking generally, I do not think that there can be any doubt in the minds of those who have followed the descriptions of rod-formation given in former parts but that the rods are protruded by forcible discharges of fluid, and all the microscopic appearances are in favour of these discharges coming from the nuclei.

Some Concluding Observations on the Nuclei.

In Part III of these retinal studies, I described in detail a migration of nuclei on a large scale through the retina.

No mention was made in that paper of the protomitotic system, which, it is obvious, must complicate this migration. The nuclei are not free, like leucocytes, to wander through the tissues, but are nodes of a reticulum continuous through the whole retina. How can we reconcile the two phenomena? Before making an attempt it may be well to describe an observation which might possibly throw some light upon the mechanism of this movement.

In the last section we described two phases in the retinal nuclei which found the readiest explanation in a pulsatory activity of the individual nuclei, an activity which drove, or assisted in driving, fluid outwards through the retina. We described extraordinary expansions of the nuclei, in which the nuclear membrane played a comparatively passive part. We have now to describe an entirely different kind of nuclear expansion, which may culminate in a complete or partial disappearance of the membrane. Now and again, under circumstances the nature of which I have not discovered, a delicate angular network is seen protruding from, or at least attached to, some of the nuclei. The threads of the reticulum, though very delicate, are fairly visible, because apparently slightly coated with staining matter, and at their nodes minute staining microsomes occur. These extra-nuclear networks seem, in the retinas in which I have found them, to be specially noticeable in the ganglionic layer (see figs. 27 *a-c*). But fig. 27 *d* shows a nucleus of the middle layer thrusting a network into the outer reticular layer, and I have already figured two cases in other layers in Part II, figs. 26 and 27. But in none of these figures did I at the time observe any filaments connecting the networks with adjacent nuclei, although such must have existed. In the first set of figures the extra-nuclear network seems to occupy the place of the granular cytoplasm commonly associated with "ganglionic" nuclei. In fig. 27 *a*, the two nuclei on the extreme right are connected by their extra-nuclear networks. In the earlier observations (figs. 26 and 27, Part II) the networks seemed to be in one case the projection of a nucleus advancing

through the outer reticular layer (cf. fig. 27 *d* of this paper), and, in the other, the trail of a nucleus that has become a rod-nucleus and has just protruded a cone.

In individual cases in which extra-nuclear networks are very strongly developed from one side, the wall or membrane of the nucleus on that side appears not infrequently as if it were dissolving (fig. 27 *c*). I have, indeed, seen a case in which a whole nucleus appeared to have lost its usually pronounced outline, and to be opening out (fig. 27 *e*).¹

It will be seen from the figures that these extra-nuclear networks were quite free of any granular cytoplasm. But the fact above stated that, like the granular cytoplasm, they are most frequently found with ganglionic nuclei, compels us to associate them in some way with the cytoplasm. It may be that they usually underlie the masses of cytoplasm which, when present, would render them, as a rule, quite invisible. Traces of a reticular arrangement of the "Nissl's Schollen" are sometimes visible (see figs. 1 and 12). They are certainly not always present when the nuclei are naked, that is devoid of granular cytoplasm, and it is only in such cases that they can readily be seen in their true form and extent. It would seem that the "Fadengerust" may be at one time a reticulum and at another a system of rays.

Returning now to the difficulties which beset the migration of the nuclei through the protomitotic system of which they form the nodes, it would be easy if the whole reticulum moved forward together, but the evidence seems to point to individual nuclei moving not only radially but tangentially (from the rim inwards) among the other nuclei. It is possible that this apparent freedom is not really great. Our sections are only snapshots of the process; hence we may see what appears to be a free movement, but is really controlled by the rest of the reticulum.

¹ The opening out of a compact central nuclear reticulum into a more open protomitotic reticulum evenly distributed throughout the cell might possibly account for the disappearance of the nucleus in red blood-corpuscles; cf. Negri, 'Anat. Anz.,' xvi (1899), p. 33.

Any freedom of movement at all must involve a good deal of slipping of the individual filaments, for each node is itself a complicated reticulum. At one time it seemed possible to find some clue to the mechanism of the movement in the extra-nuclear networks, in which there appears to be a temporary dissolution or loosening of the intra-nuclear networks. But although these extra-nuclear networks appeared in the migrating nuclei shown in Part II, Pl. 31, figs. 26 and 27, in most cases the nuclei can be seen passing through the outer reticular layer with clean, hard outlines, and sometimes with clearly defined amoeboid changes of shape. The most remarkable cases of this were seen in the large retinal nuclei of *Ceratodus* and *Protopterus* (see fig. 28), but it can frequently be seen in nuclei passing through the outer reticular layer, e. g. in the cat many of them were shaped like large-headed pins (see figs. 20 *b* and 25). I do not now think the two phenomena have much more to do with one another than that both are dependent upon a great power of slipping on the part of the protomitotic filaments. In fact, it looks as if the reticulum is the very reverse of rigid; that, in spite of its complicated nodes, in life its filaments move freely upon one another.

One more problem relating to the retinal nuclei must claim a moment's attention. What is the origin and the function of the numbers of minute nuclei found, especially in young Mammalian retinas, in the ganglionic cell-layer, and mostly on its inner side? See, for instance, fig. 25, which shows them in a young cat. Others are shown in figs. 2 *b*, 3 *c*, *d*, and 26 *g*. They are mostly very minute. If they happen to be large they are usually very much indented, as if they were fragmenting (see figs. 26 *g*, and 3 *c*). They are almost devoid of chromatin contents, and frequently look like clear empty vesicles. A comparative study which might throw light upon them must be a work of the future. I have so far only endeavoured to see if they were linked on to the retinal protomitotic system, but without arriving at any positive result. The few filaments I succeeded in seeing coming from them were always lost sight of in the surrounding tissue. If

they belong to the retinal protomitomic system, one would expect them to be in the line between the nerve-layer and the rods. But there is no reason why there should not be in any organ subsidiary systems regulating vegetative processes within the organ, and apart from the specific functions of the organ itself.

Summary of the Leading Morphological and Physiological Characters of the Protomitomic System, as above described, in the Retina.

The morphology of the retinal protomitomic system has already been summarised in the diagram fig. 22. It is a continuous reticulum of nearly invisible fibrils, which become visible when coated with other matters. I have hesitated to call them *linin* filaments because, as I shall show elsewhere, that term is at present applied to substances quite distinct from these filaments. But it is undoubtedly the proper application of the word. It underlies the whole retina; the nuclei are its nodes. Each node is a still closer reticulum in which chromatin accumulates, and with the chromatin a quantity of clear fluid—nucleoplasm—which turns the node into a turgid vesicle. This chromatin, massed on the fibrils of the nodes, renders the latter not only visible but conspicuous objects. Distally, the filaments of the retinal protomitomic system run out as a fringe, not of free threads like cilia, but gathered into groups by supporting vesicles, the rods. Proximally, the filaments are gathered as the “*Neuro-primitivfibrillen*” into the nerve-strands which connect the retina with the brain.

The physiological characters of the protomitomic system, as gathered from our study of the retina, have still to be summarised.

1. Since the protomitomic reticulum connects the optic nerve with the fibrillation of the rods, its component filaments are nervous.

2. Since the intra-nodal reticulum seems to have the power

of contracting, and as its filaments are continuous with those connecting the nodes together, we are safe in assuming that the protomitomic filaments are contractile.

3. As the rods are protruded from the retina and the filaments are pushed out along them, no matter how long the rods are, the filaments are capable of growth.

4. The apparent openings out of the nodal reticulum to form the extra-nuclear networks suggest the possibility of a somewhat free slipping of the junctions of the protomitomic filaments. And this has also to be assumed in order to account for the migration of individual nuclei, for the filaments which function as the paths for the nerve-stimuli must be thought of as permanently continuous.

These seem to be the chief functional attributes of the protomitomic filaments; they are capable of conducting nerve-stimuli, they are contractile, they can grow, and they can move freely upon one another. But it is probable that, by themselves, they can do none of these things, and that the vital phenomena we have mentioned as apparently attributable to the filaments of the protomitomic system, are only so when it is associated with the other principal constituents of protoplasm. These are four.

Probably the most important, and certainly the most intimately associated with the fibrils, is the chromatin. This is found either massed in the close nodal or nuclear networks, or streaming along the filaments from node to node. In no case does it appear to leave the filaments.

The next is apparently the clear fluid matter which is closely associated with the chromatin, and makes the nuclei turgid vesicles.

We then have the granular cytoplasm, which tends to aggregate round the nuclear nodes, probably as nutritive material; and lastly, the clear glassy strands of the syncytial framework, which seem to act as supports. The protomitomic filaments either pass through these membranes, or may be bent by them (see fig. 13 *b*), or they may run along in some close association, and yet in such a way as not to hinder the

passage of chromatin upon them. I refer to the fibrils running in or upon the walls of the rods, and also to the nerve-fibrils in or on the membranes of the supporting framework of the nerve-strand.

These are the leading facts with regard to the morphology and physiology of the protomitotic system of the retina, so far as they have been revealed by these researches. Not many of them are new. As we have already noted, the "prickles" joining the nuclei to the cytoplasm were described as universal phenomena by Heitzmann, and have been frequently figured since. The existence of intercellular bridges between the cytoplasmic masses which usually surround the nuclei have been recorded sufficiently often to justify the assumption that they are fundamental factors in multicellular organisms. The existence of a fibrillar substance underlying the cytoplasm, and even running in the walls of the alveoles in those cases in which the cytoplasm appears to be a foam structure, completes the series. If we put these together, as Professor Macfarlane has tentatively done for plant tissues, and as we are now completely justified in doing, we arrive at the protomitotic system which the retina has just clearly and directly revealed to us, owing to the fact that so many of its nuclei are unobscured by any granular cytoplasm. Further, that the nerves were bundles of primitive nerve-fibrils has long been known. That these primitive fibrils occasionally run into the intra-nuclear reticulum has been seen by several observers, but, owing to the element of chance, first in finding the filaments preserved, and then, if preserved, in the right physiological condition to be rendered visible under ordinary powers of the microscope, confirmation has not been forthcoming. The striation of the rods was well known, and its connection with the primitive nerve-fibrils was suggested by Max Schultze. The expulsion of nucleoplasm from the nuclei has been described, and the contractibility of the protomitotic filaments has been maintained, in order to account for some of the phenomena of mitotic cell division, and for the movements of leucocytes. And, lastly, the growth of the primitive nerve-

fibrils is a known phenomenon in the process of nerve regeneration. Thus, in almost every point, the ground has been trodden by previous workers. Most of their observations have, however, remained isolated and fragmentary. The foregoing study of the retina has enabled us to link them all together.

There remains, however, a whole field of facts and theories relating to protoplasmic structure based largely upon observations of an entirely different character. All our observations are purely microscopic, and it may be of interest for a moment to compare the results with those obtained by chemistry or by experimental physiology. Professor Verworn has recently attempted to co-ordinate them by means of the biogen hypothesis.¹ According to this, there are certain very complicated molecules, the "biogens," whose activities in presence of certain other substances, oxygen on the one hand and nutritive carbohydrates on the other, may be made to account for most of the known phenomena of metabolism. These molecules are said to have their chief seat in the cytoplasm and not in the nucleus, which is, in essence, a reserve dépôt for the oxygen and other chemicals necessary to enable the biogens to perform what is required of them for the vital processes with the carbohydrates derived from food. The real test of this theory as a working hypothesis must naturally come from physiological chemistry, but morphology cannot be left altogether out of account. One of the chief problems of the biogen hypothesis is how to picture the several factors distributed in space within the cell so that they may always be in contact with or within reach of one another for their mutual reactions. It seems to me that the description above given of the fundamental structure of protoplasm may possibly supply an answer. If the protomitomic filaments are strands or chains of biogens, then we have these latter, with a specially dense and usually more passive part of their reticulum, immersed in the reserve dépôt of the chemicals necessary for their activity (the nucleus).

¹ Max Verworn, 'Die Biogen-Hypothese,' Jena, 1902.

From this reserve, and coated with a thin layer of its stored-up material, they radiate outwards in all directions into the surrounding mass of the granular cytoplasm supplied by the food. By this method of arrangement, the radiating network, which takes the leading part in all vegetative processes, could always be supplied with the two different kinds of substances on whose chemical unions its "life" depends.

Returning to our own sphere, the morphological unit in protoplasmic structures is the protomitotic system, while what is ordinarily called the cell is simply a centre of physiological activity for this system. The number of centres in all probability varies according to the extent of the system or according to the intensity of its functional activities.

This brief summary clearly assumes that a protomitotic system underlies all protoplasmic structures. For the present, it is sufficient to show that that assumption is justifiable. The retina is an organ of the body, and it is not at all probable that its fundamental constitution should be different from that of the organism of which it is but a part. Peculiar as the general structure of the organ may be for its special function as a retina, it results from a modification of the same formative tissue from which all the other organs have arisen. Further, the connection with the rest of the organism by means of the optic nerve compels us to believe that the nerve-fibrils which run into the nuclei of the retina, and then on from nucleus to nucleus, must themselves have come from nuclei of the central nervous system. And further, reasoning in this way from the central nervous system to other organs, we are forced to conclude that protomitotic systems underlie all the organs of the body, and that they also, like the retina, are connected with the protomitotic system of the central nervous system by bundles, often of considerable length, of protomitotic filaments—that is, of primitive nerve-fibrils. If this deduction be correct, a new light is thrown on the morphology of the nervous system.

That this universality of the protomitotic system as the essential structural element in protoplasm is not a mere

inference, but admits of demonstration, will shortly be shown in another paper.

EXPLANATION OF PLATES 27—29,

Illustrating Mr. H. M. Bernard's paper on "Studies in the Retina."

In all the figures *m. l. i.* = membrana limitans interna; *m. l. e.* = membrana limitans externa; *i. r. l.* = inner reticular layer; *o. r. l.* = outer reticular layer; *n. l.* = nerve-layer; *s. s.* = strand of the retinal syncytium; *b. v.* = blood-vessel.

FIG. 1.—From the retina of a young cat (Perrenyi). A large ganglionic cell with the cytoplasm filling a syncytial chamber. The "Nissl's Schollen" clearly connected with the nucleus, and as if arranged as a reticulum throughout the cytoplasm. Cf. Fig. 12 and also Fig. 26.

FIG. 2.—Retinal ganglionic nuclei. *a* and *c* from a rat three years old (Perrenyi), *b* from a rat four days old (Flemming's fluid), showing what appear to be small, apparently fragmenting nuclei with hardly any chromatin contents. *a* shows a single mass of granular cytoplasm associated with three small nuclei; *c* shows a large vesicular nucleus with dispersed chromatin, and near it a contracted nucleus with vacuoles in the *i. r. l.* Cf. Fig. 3, *a* and *b*.

FIG. 3.—Retinal ganglionic nuclei. *a*. Rat, three years old (Perrenyi). *b, c, d*. Young cat (two days) (Perrenyi). (Fig. 25 shows more of the same section as *d*.) *a* and *b* show vesicular and contracted nuclei; *c* and *d* nuclei with very scattered chromatin contents, and apparently fragmenting.

FIG. 4.—From the retina of a salamander (corrosive sublimate). A thin tangential slice of a nucleus of the middle layer, showing the matted branchings of the intra-nuclear reticulum without any associated cytoplasm or even continuous nuclear membrane.

FIG. 5.—From the retina of a mouse (Hermann). Ganglionic nuclei, as a rule without granular cytoplasm, most with chromatin protruding, and often as if streaming away.

FIG. 6.—From the retina of a stickleback (Lindsay Johnson's fluid). This figure shows two ganglionic nuclei with their connecting filaments running to the primitive nerve-fibrils seen in the transverse section of the nerve-strand. In this section the nuclear connections could be traced very clearly nearly through the retina (cf. Fig. 17 *a*, from the same retina).

FIG. 7.—From the retina of a plaice six inches long (Flemming). A ganglionic nucleus with granular cytoplasm streaming from one side, and with the threads of the intra-nuclear network radiating outwards, some of them going towards the nerves with beads upon them.

FIG. 8.—From the human retina (Perrenyi). The deeply stained primitive nerve-fibrils become faint before reaching the nuclei, but the connection can be made out. All the filaments run from nucleus to nucleus. All the nuclei here shown are devoid of granular cytoplasm.

FIGS. 9–11.—From the human retina (Perrenyi).

FIG. 9 shows the connection between the nuclei and the primitive nerve-fibrillæ. The distal connecting filaments apparently obscured by granular cytoplasm.

FIG. 10.—The granular cytoplasm is all on one side, and contains "Nissl's Schollen" in obvious connection with the nucleus, but streaming away distally; filaments from the nucleus plunge straight into the inner reticular layer (cf. FIG. 15).

FIG. 11.—Several of the nuclear filaments running to the nerve pass through the granular cytoplasm, and are visible because dotted with beads; near the edge of the cytoplasm the beads become large shapeless clumps. Note the contrast already shown in FIGS. 8 and 9 between the thick staining primitive nerve-fibrillæ and the connecting filaments.

FIG. 12.—From the human retina (Perrenyi). A group of "ganglionic" nuclei joined together by filaments which are continuations of the intra-nuclear networks; proximally, the filaments run into the fibrils of the nerve-layer, *n.l.*, which are shown cut either across or slightly obliquely. Three of the nuclei have granular cytoplasm on their distal sides. The "Nissl's Schollen" are seen very clearly associated with the nuclear filaments, and then appear comparable with such masses of extra-nuclear chromatin as are shown in FIGS. 18 *a*, *b*, *c*.

FIG. 13.—From the retina of a salamander (corrosive subl.). Nuclei joined by filaments which can only be seen by very careful focussing; the filaments pass through the synektial strands, *s.s.*, and are sometimes bent where they go through.

FIG. 14.—From the retina of a salamander, taken out of the body-cavity of the mother (Flemming). The nuclei packed tightly together, and without any cytoplasm, granular or synektial, traceable between them. The intra-nuclear networks run into one another.

FIG. 15.—From the retina of a young plaice two inches long (Flemming), showing the inner reticular layer as a "Punksubstanz" with a subtle radial striation, clearly seen in this case to be due to nuclear filaments passing through the layer and running into nuclei of the middle layer.

FIG. 16.—From the retina of a frog (boiling corrosive), showing the nuclei

of the middle layer run together as amœboid bodies joined by their processes into a network. This is apparently one of the effects produced by the violence of the fixative, the other being the balling together of the nuclei into small globules of refractive chromatin.

FIG. 17.—Retinal nuclei of the middle layer showing connecting filaments. *a*. Stickleback (Lindsay Johnson's fluid). *b* and *c*. Plaice (Perrenyi) showing stages in the contraction of the chromatin within the nuclei. *d*. Mouse (? Perrenyi). *e*. Frog (osmic vapour).

FIG. 18.—From Amphibian retinas showing the nuclei joined together, the connecting filaments made visible by clumps and coatings of staining matter. *a*. From a tadpole from Table Mountain, fixed 2 a.m., four nuclei, three in the middle layer and one a rod-nucleus; with two masses, one very large, of extra-nuclear chromatin; the large mass seems half arrested by the outer reticular layer (*o. r. l.*). *b*. From the same, shows the nuclei of middle and outermost layers not only connected inter se, but the nuclei of the one layer connected with those of the other through the outer reticular layer; one large mass of extra-nuclear chromatin. Such masses are common, and have, in the human retina, been mistaken for small nuclei. *c*. From a toad tadpole fixed at 2 a.m., with small irregular clumps of extra-nuclear chromatin massed on the filaments. *d*. From a frog tadpole fixed 10 p.m., showing a nearly complete nuclear connection from the inner reticular layer on to the rods.

FIG. 19.—From the retina of a plaice, six inches (Flemming), from same eye as Fig. 17 *b*, *c*. Two nuclei very highly magnified within the outer reticular layer on their way to become rod-nuclei; they send filaments towards the nuclei of both middle and outer layers.

FIG. 20.—From the retina of—*a*, cat, two days old (Perrenyi); *b*, cat, six weeks old (Flemming), showing the gradual lineal arrangement of the clumps of chromatin; *c*, *d*, old cat, thirteen years (Perrenyi), *c* showing the filaments connecting the chromatin clumps, and *d*, the gradual change in the arrangement of the chromatin as a nucleus passes through the outer reticular layer, *o. r. l.*, to become a rod-nucleus; *e*, *f*, rod-nuclei of mouse; *f*, fatigued and with loss of chromatin.

FIG. 21.—From a human retina. Rods showing in *a* a specially clear connection between the filaments striating the rods and the intra-nuclear reticulum. In *b* bundles of fibrils come down from the upper tiers of the nuclei. *a* is a rod with a swollen inner limb, usually called a cone, but probably having no morphological significance.

FIG. 22.—A diagram showing how the primitive nerve-fibrillæ reach the rods through the intermediary of the retinal protomitotic system; for further details see text, p. 326. See also p. 339 for the meaning of the asterisk.

FIG. 23.—From the retina of a frog tadpole (eye diameter 4 mm.) fixed in Perrenyi's fluid at 12 midnight. Selected groups (*a*, *b*, *c*) of elements near

the rim of the retina, *c* being nearest to the centre, showing rod-vesicles being protruded from the distal ends of the radial attachments of the spindle-shaped cells which persist at the rim of the retina. On the extreme right in *a* two nuclei are seen connected together, and in *b* two vesicular protrusions from nuclei are seen, and into them radiating strands come from the nuclei.

FIG. 24.—A diagram representing what I conceive to be the change which converts the columnar epithelium of the pars ciliaris retinæ into a thick layer of closely packed spindle-shaped cells, this layer being later broken up into the normal zones of the retina by the wandering inwards towards the axis of the nuclei of these cells. The protrusion of fluid-vesicles beyond the *membrana limitans externa* is already foreshadowed by a distal accumulation of fluid in the otherwise undifferentiated cells of the columnar epithelium, which may be occasionally seen.

FIG. 25.—Part of a radial section through the retina of a young cat, two days old (Perrenyi's fluid), to show the proximal nuclei nearly all devoid of chromatin, which is massed in the distal or rod-nuclei. The inner or ganglionic layer is of enormous thickness and full of small vesicular nuclei, many apparently fragmenting. Fig. 20 *a* is from the same eye.

FIG. 26.—A small selection of retinal ganglionic cells to show how, at times, the nucleus and its granular cytoplasm may have nearly the same shapes. *a-f*, from old cat (Flemming); *g*, young cat, six weeks (Perrenyi); *h-q*, young dog (Flemming). They illustrate also the arrangement of the "Nissl's Schollen" which may at times form a series concentric with a series of chromatin clumps within the nucleus (see *g*).

FIG. 27.—Extra-nuclear networks (see p. 351). *a, b, c, e*. From the retina of a mouse tired out by exposure to an arc lamp (Perrenyi); *d*, of a rat, young adult (Flemming); *a, b, c, e*, a group of "ganglionic" nuclei; on the right in *a*, the same network is common to two nuclei. Very similar phenomena were also seen in a wild mouse fixed in corrosive sublimate, only the networks were not quite so sharply defined. *c*. From the same, shows a large ganglionic nucleus with two extra-nuclear networks; that on the right seems to have dissolved the wall. *e*. From the same, showing a nucleus with the wall all round apparently dissolved. *d*. From a rat, young adult (Flemming), showing a nucleus of the middle layer passing through the outer reticular layer with an extra-nuclear network preceding it (cf. figs. 26 and 27 of Part II). Two stellated nuclei of the rod-layer are also shown (cf. Figs. 20 *c, d, e*).

FIG. 28.—From the retina of a Protopterus (Flemming), showing two nuclei passing with amœboid movements through the outer reticular layer to become rod-nuclei. The rod-nuclei protrude a long way through the *m. l. c*.

The Bionomics of *Convoluta roscoffensis*, with Special Reference to its Green Cells.

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With Plates 30 & 31.

CONTENTS.

	PAGE
Section I.—INTRODUCTION	364
Section II.—THE FOOD OF CONVOLUTA	368
1. Previous Observations	368
2. Observations of the Authors	370
3. Photosynthesis	375
4. Appendix : Assimilation Experiments	377
Section III.—THE DEVELOPMENT OF THE "GREEN CELLS".	378
1. The Occurrence and Significance of Chlorophyll in Animals	378
2. Views of Previous Writers on the Green Cells of <i>Convoluta</i>	382
3. The Origin of the Green Cells	383
4. The Development of the Green Cells from Colourless Pre- decessors	390
5. The Influence of Light	392
Section IV.—THE TROPISMS OF CONVOLUTA	394
1. Geotropism	395
2. Thermotropism	396
3. Phototropism : the Influence of Background ; periodic tidal effect	397
4. The Influence of Monochromatic Light on Phototropism	402
5. Reactions to Two or More simultaneously Applied Stimuli	405
6. Rheotropism, Thigmotropism : Applications	406

	PAGE
Section V.—ECOLOGY OF CONVOLUTA	407
1. Position of the Colonies of Convoluta	407
2. The Factors that regulate the Formation and Position of the Colonies	410
3. Variations in the Constituent Patches of a Colony	412
4. General Phenomena of Reproduction and Development	414
Section VI.—SUMMARY	418
Section VII.—LITERATURE	424
Section VIII.—EXPLANATION OF THE PLATES	428

Section I.—INTRODUCTION.

Convoluta roscoffensis is a green Turbellarian peculiar to Brittany, along whose coasts it is distributed intermittently. It is a slender, elongated, ciliated worm of sedentary, gregarious habit.

Though the individual *Convoluta* is, on the average, not more than 4 mm. in length, it occurs in such vast numbers as to form conspicuous, dark, "spinach-green" patches on the shore. These patches, lying well up the beach within the tidal range, may be so small as to be barely recognisable, or so big as to form an almost continuous band, extending over fifty or even a hundred yards. The general rule, during the summer, is for colonies of *Convoluta* to occupy a number of well-defined, isolated stations separated from one another by barren stretches. Each colony consists of one patch or of a group of patches.

At night, the colonies sink beneath the surface of the sand even at low tide; only on bright moonlight nights may a few individuals of a colony be met with on the surface of the sand. During daylight the colonies rise up from below ground, and appear on the surface soon after the ebbing tide has left it. There they remain, the colony as a whole inert, but many of its inhabitants in active movement within its borders, till the returning tide covers, or is about to cover them.

The strong characteristic odour of *Convoluta* affords a means of detecting colonies too small to be seen.

Geddes discovered that *Convoluta* contains a poisonous substance. A dead *Convoluta* speedily kills a mass of healthy individuals if introduced into their midst. This toxic substance may be the means of securing such a patent organism from attack by other littoral animals. Up to the present time the only animal known to prey on *Convoluta* is a species of *Plagiostoma*.

Convoluta roscoffensis offers strong contrasts to other Acoelous Turbellarians. They are short; it is elongated. They are solitary, active, retiring, and odourless; it is gregarious, sluggish, and obvious to sight and smell. More striking differences still are those of nutrition. The allies of *Convoluta* are voracious feeders; whilst it, according to previous investigators, does not feed, but relies, so it is asserted (von Graff, 1891; Haberlandt, 1891; Georgevitch, 1899), on material manufactured by the green cells which form a dense "tissue" in its body.

It is not, however, only by reason of its possession of green cells that *Convoluta* is unique among its fellows. Other Turbellarians, and also, as is well known, other animals of various classes, are possessed some of green, some of brown cells, which, it is generally assumed, offer welcome contributions to the diet of the host in which they reside. Its uniqueness consists in this—that as a consequence of, or side by side with, the appearance of its green cells, the habits of *Convoluta roscoffensis* have become completely different from those of any of its allies.

Convoluta has been the subject of investigation by various observers, chief among whom are Geddes, Delage, von Graff, Haberlandt, and Georgevitch. Geddes (1879—1881) has shown that the green cells contain chlorophyll, that they evolve oxygen in the light, and at the same time store the superfluous products of photosynthesis as starch. Delage's classical paper (1886) described for the first time the nervous system of *Convoluta*. Von Graff (1882—1891) has dealt almost exhaustively with its anatomy, and incidentally with the more striking features of its ecology. Haberlandt (1891),

working with material sent to Gratz from Roscoff, has described the geotropic and phototropic reactions of *Convoluta*, and has figured and carefully described the histological peculiarities of the green cells. Georgevitch (1899), in the course of a research on the embryology of *Convoluta*, has experimented on its development. Geddes, von Graff, Haberlandt, and Georgevitch are agreed that *Convoluta* does not ingest solid food, but depends for its food on the carbohydrate and proteid-synthesising processes of the green cells. In support of this view, Geddes (1879 B) points to his observation that *Convoluta* dies quickly—within three days—when kept in the dark; von Graff (1891) to his failure to discover any traces of food in *Convoluta*, and to the paucity of wandering cells; Georgevitch (1899) to the mortality which he notes among just hatched animals when secured, as he supposes, from infection by being placed in filtered water.

In the present paper we bring forward new facts which show that this view—that *Convoluta* is obligately parasitic on its green cells—is not well founded; we prove that the above-mentioned observations on which this view is based are erroneous, and offer a somewhat different view of the relations which obtain between *Convoluta* and its green cells.

The origin of the green cells has been the subject of speculation on the part of Haberlandt and Georgevitch. Haberlandt considers the alternative possibilities of external or internal origin. He inclines to the view that, whatever the primitive origin of the green cells may have been, they have been so domesticated to the service of *Convoluta* as to have lost the power of independent existence, and to have come now to be transmitted in the egg, perhaps in some way like that in which the chloroplast of a green plant is transmitted in the egg as a colourless plastid. Georgevitch, relying on the negative results of his experiments, concludes that young colourless *Convolutas* become green by infection from the sea water.

By culture experiments, and by observations on young and

adult *Convolutas* as well as on the eggs, we show that the evidence is against Haberlandt's theory; and that Georgevitch's view of direct infection, though probably correct, is insufficient, inasmuch as there is no infection of *Convoluta* by a green cell. We show that the problem of infection is at once more complex and more difficult than has been supposed. More complex, inasmuch as the green cells of *Convoluta* develop from colourless cells within its body. More difficult, because it is impossible, by ordinary means, to cultivate *Convoluta* in a sterile medium; and this not because *Convoluta* does not hatch out and grow well in filtered or heat-sterilised sea water—this it does,—but because the egg-capsule is far from sterile, being, in fact, infested by all manner of green and colourless cells, spores, and even diatoms.

Though we have failed to isolate an infecting organism, we bring forward evidence in favour of the theory that the green cells of *Convoluta* are the result of an infection. This evidence is derived from experiment, and from observations on the position in which the colourless progenitors of the green cells are first found in the body of the recently hatched animal. We trace the stages in the development of these colourless cells into the green cells, and the migrations of the latter through the body to their final disposition as a dense green layer just beneath the skin.

Finally, we supplement and extend the observations of Haberlandt on the tropisms of *Convoluta*, and endeavour to show how these tropisms co-operate to form the habits and determine the distribution of the animal.

The research was commenced at Roscoff in the summer of 1901, and since then has been carried on at Trégastel (Côtes du Nord), and in the laboratories of Owens College, Manchester, and University College, Reading.

Section II.—THE FOOD OF CONVOLUTA.

1. Previous Observations.

Whereas diatoms, rotifers, and other solid ingesta are constantly found in allied Turbellaria, previous observers have failed to demonstrate the presence of "food" in the bodies of *Convoluta roscoffensis*.

Geddes (1879) kept *Convoluta* alive for four to five weeks without food. Haberlandt (1891, p. 88) did not find a single specimen containing food taken up from without, although he kept *Convoluta* in a well-stocked aquarium at Gratz. Von Graff (1891, p. 70) states that of all the living and sectioned *Convoluta* he examined, only one or two contained any foreign bodies, and these foreign bodies were without exception discharged mouth-pieces of the "bursa." The paucity of phagocytes in the body of *Convoluta*, and the supposed barren nature of the sand, also led von Graff to conclude that this animal did not live on animal food. Georgevitch (1899), after examining larval, adolescent, and adult *Convoluta*, states (p. 358) that "it is certain that *Convoluta* does not take nourishment (i. e. from without) either in the embryonic or adult stages."

These authors agree that *Convoluta* is nourished by means of the green cells which form an assimilating tissue in the superficial parenchyma. Geddes (1879) has shown that these green cells produce starch, and inasmuch as he found that *Convoluta* dies rapidly when placed in the dark, but lives for weeks in the light, he concluded that *Convoluta* lived upon the starch of the green cells. Haberlandt (1890) offered a more elaborate explanation of the mode of nutrition. Failing to find any trace of digestion of the green cells as a whole by the animal tissue, and observing the fragmentation of these green cells when *Convoluta* was firmly pressed between slide and cover-slip, Haberlandt inferred that *Convoluta* fed by digesting such fragments, by digesting starch

set free from the green cells, and possibly also by osmotic translocation of a soluble carbohydrate from the green cells to the surrounding tissues.

The special adaptations of *Convoluta roscoffensis* have been regarded by previous writers as contrivances for ensuring the continued assimilation by the green cells and the nutrition of the animal.

Its body has become elongated and flattened, exposing a great extent of surface to the light. Its station is high up on the beach, where the greatest amount of light and yet a sufficiency of moisture may be obtained. It forms vast inert patent colonies protected from attack by the nauseous alkaloid (probably trimethylamin) which, as Geddes has shown, *Convoluta* excretes. In these several ways, *Convoluta* stands in marked contrast to its retiring submerged troglodyte allies; and it has been assumed that the special mode of life of *Convoluta* and its peculiar tropisms adapt it for its special holophytic mode of nutrition.

That its station high up on the beach ensures to *Convoluta roscoffensis* a prolonged daily light exposure is clear enough. That its flattened form and peculiar tropisms favour photosynthesis is also certain. Nevertheless the view held by previous authors that *Convoluta* is holophytic in its mode of nutrition is either an inference from these facts of adaptation, or is based on negative evidence, viz. the absence of food in the bodies of the animal. We show that the evidence is unsound, and that we must interpret the relation between the "green cells" and the animal in a different way.

Before recording our own observations we may remark that *Convoluta* is not the only animal in which observers have failed to demonstrate the presence of food, and it is noticeable that the presence of yellow or green cells is frequently correlated with this abstemious habit. For example, no food has been found in the tissues of certain adult *Radiolaria* (Brandt, 1882), *Ciliata* (Entz, 1881-2), *Hydrocorallines* (Hickson, 1889), *Madreporaria* (Hickson,

Bourne, Fowler in litt.¹); and it has been suggested (Brandt, 1882; Hickson, 1889) that these animals subsist, at least during their adult stage, on the plastic products of their yellow or green cells. Proof of such holophytic nutrition is, however, still to seek. The experiments made by Brandt (1882) on anemones and Radiolaria, and supposed by him to afford the desired proof, have been repeated by Famintzin (1889, 1891), and have been shown to be susceptible of a different explanation. Famintzin concludes that, if the green and yellow cells of these animals subserve nutrition, this nutrition is only effected by the digestion of the coloured cells and their contents. Nevertheless the translocation theory has been and is widely accepted. If, then, we can show that the highest expression of "symbiosis," that seen in *Convoluta*, is not accompanied by abstention from active feeding on solid bodies, we shall have succeeded not only in refuting a general error, but in reopening the question of nutrition in other cases of animal and algal associations.

2. Observations of the Authors.

Convoluta feeds and feeds voraciously. From the time of hatching to the period of maturity it enjoys a remarkable catholicity of taste. Diatoms, unicellular algæ, spores of all kinds, grains of sand, and colonies of bacteria are ingested with equal avidity. Nor does it refuse artificial "food." Litmus, methylene-blue, congo-red, starch, lamp-black, and indigo are absorbed and distributed as though they were nutritious substances. The accompanying figures (Pl. 30, figs. 4—6) demonstrate the presence and "digestion" of various of these substances.

When the period of maturity arrives, *Convoluta* adopts a new mode of nutrition. Almost every adolescent and adult specimen of a colony, if examined at low tide, contains one or more rounded brown masses in the central tissue of the

¹ Duerden, 'Memoirs Nat. Acad. Sci.,' Washington, vol. viii, 1902, "West Indian Madreporian Corals," has suggested that corals feed at night, but has found no food.

body. These are the remains of green cells from which the digestible portions have been removed (Pl. 31, fig. 7).

The general features of the nutrition of *Convoluta roscoffensis* may be stated in the following manner:—In the embryonic and early larval stage, the animal feeds upon its reserve materials. After hatching, it is for a time—that is, up to time of functioning of the green cells—heterotrophic. It then passes through a long period, during which it subsists on diatoms and other ingested substances, possibly also on organic food derived from its green cells; that is, assuming that *Convoluta* adopt both these methods, it is myxotrophic. Finally, in the mature stage, it derives all its food from the green cells directly by digesting them, and possibly also indirectly by extricating plastic material from them. Up to the present, however, there is no evidence that *Convoluta* derives any food by the last means.

It is often assumed that the number and variety of forms of life are diminished in the upper part of a sandy shore as compared with the more continuously submerged lower zones of the beach. Von Graff, for example, when referring to the abstention of *Convoluta roscoffensis* from food, states that its “life in sterile sand is, at all events, unfavourable to the assumption that *Convoluta* feeds on an animal diet” (1891). *Convoluta*, however, does not live in sterile sand. The variety and numbers of the fauna and flora of the *Convoluta* zone is remarkable. Foraminifera and ciliate Protozoa, Nematodes, Copepods, and Turbellaria are the chief and most constant forms of animal life; whilst bacteria, diatoms, brown and green algæ of simple forms, are the main kinds of vegetable life. In addition to these sources of food, the rich grazing grounds provided by *Convoluta* itself must be mentioned. We refer in Sect. V to the formation of the egg-capsules simultaneously by large numbers of a colony, and to the concomitant casting off of the hinder end of the body. The capsules attract large numbers of diatoms, and in time become almost covered with colonies of simply organised algal cells. The detached

hinder ends disintegrate whilst attached to, or in the neighbourhood of, the capsules, and attract swarms of bacteria and ciliate Infusoria. Thus at the time of hatching *Convoluta* finds itself surrounded by an inexhaustible store of food (see Pl. 30, fig. 3). If we picture the vast numbers of egg-capsules that are laid by these extensive colonies; if we add to the capsular fauna and flora the free living forms of life that swarm in the sand; and if, further, we add the organisms that doubtless infest the capsules of these free living forms; we shall have some idea of the illimitable supplies of food that these stretches of fertile sand afford to their inhabitants.

We now describe the apparatus by the aid of which *Convoluta* ingests, digests, and circulates its food. The larva—that is, the animal just after hatching—possesses a central nucleated tissue which forms a sponge-work, the meshes being composed of a firmer substance, with nuclei at intervals, and containing a more fluid plasm. This tissue is strongly developed in the hinder half of the body, and forms a conspicuous protrusion on the ventral surface. It appears to communicate with the exterior by a mouth placed almost in the centre of the under surface. Two concentric delicate markings probably represent the mouth, but the appearances are such as do not justify a definite statement. Such as they are, they point to a sphincter which is kept closed, and is presumably only relaxed at the moment of ingestion or ejection of food or of remains of food. In later stages the mouth and pharynx are easily recognisable at this point.

In the central syncytium there are, even at the time of hatching, one or more nucleated delimited masses of cytoplasm. At an early stage two of them are present just above the mouth. These are the wandering cells, which ingest the food and then move backwards to the thicker, hinder part of the body. In larval *Convoluta* they may be seen in that position enclosing algæ or other nutritive substances. Frequently they fuse to form a multinucleate mass in this hinder region. Such a structure is constantly to be seen in

Convoluta during its first fortnight's free existence, and is figured on Pl. 31, figs. 12—16. Within this mass digestion occurs. Algæ remain for a long time unaltered, but diatoms are soon resolved into a brown granular fluid and empty valves (Pl. 31, figs. 10, 11). Other remains of food are seen in the dumbbell-shaped masses seen in fig. 9.

The wandering cells circulate as well as digest the food. Diatoms in process of disintegration are met with in the anterior part of the body and in the lateral parenchyma, as well as in the central syncytium, or "gut" (Pl. 31, fig. 9). The close contact between such food-laden wandering cells and the green cells suggests that the latter may in this way receive their nitrogenous supplies.

The course of the food may also be followed by the use of litmus, indigo, methylene-blue, lamp-black, and other substances. Methylene-blue, for example (fig. 6), is taken up by wandering cells, and after a time appears in a diffused fluid form in the meshes of the syncytium. Litmus is carried in great quantities to the peripheral parenchyma. Congo red is equally well distributed by the agency of the active cells (Pl. 30, fig. 5). Sodium sulphindigotate is treated in the same manner, and though it is often used as a natural injection to demonstrate excretory tissues, we have seen no trace of an excretory system. After several months of daily examination of *Convoluta* at all stages of development, and after the employment of substances that are specifically excreted in other animals, we have not seen a flame-cell or a canaliculus. We have, however, repeatedly seen the "pulsellæ" observed by Geddes (1879) and Delage (1886), both in larval and adult forms, but we are unable to suggest what their nature or function may be (Pl. 31, figs. 17, 18).

Whereas the outer surface of *Convoluta* is strongly alkaline, the central syncytium, or "gut," is strongly acid. The former reaction is probably due to the secretion of the skin-glands, which, according to Geddes, contain a volatile base, probably trimethylamin, the source of the potent smell and poisonous action of *Convoluta*. The latter reaction can

be demonstrated by the use of congo red, which becomes altered to blue within the gut (Pl. 30, fig. 5), and by pressing the animal on litmus-paper. Even a just-hatched *Convoluta* gives, by the latter method, a very decided acid reaction, plainly visible to the naked eye. The reaction of the gut of larval, adolescent, and adult *Convoluta* is equally acid. We have already stated that mature *Convoluta roscoffensis* contains brown masses, the remains of digested green cells. This mode of nutrition is strikingly similar to a process which is known to occur in lichens. It has long been known that, in certain species, the algal cells of these organisms may be invaded by the hyphæ of the fungus. Peirce (1900) regarded the algal cells as at first parasitic on the fungus, and subsequently the fungus parasitic on the algæ. More recently it has been shown (Elenkin, 1901) that in heteromorous lichens the haustoria-like projections of the fungal hyphæ digest the living substance of the greater proportion of the green cells. The débris of the digested cells takes the form of brown masses, and the phenomena are interpreted as proving that in such cases endosaprophytism rather than "symbiosis" expresses the relation between fungus and alga. It is also known that in *Hydra viridis* the green cells, after a time, fail to resist the disintegrating action of the endoderm cells, become digested, and their remains form brown or reddish matter (Kleinenberg, 1872, p. 6; Beyerinck, 1890). In none of these cases has it been shown that the plastic materials stored in the coloured cells are absorbed by the animal or by the fungoid tissue, though the presumption is strongly in favour of this view.

If, in the long interval of immaturity during which we know that *Convoluta* is absorbing food from without, it is also making use of the plastic materials stored in its green cells, this should be capable of proof by placing the animal under such conditions that its external sources of supply are curtailed, and that loss of plastic material can be estimated. This may readily be done by putting *Convoluta* in a limited quantity of water free from sand, or in a current of clean

sea water, and cutting off the light. The results of such experiments show that the starch of the green cells—the form in which the carbohydrate material is stored—disappears with extreme slowness. During the first day or so the loss of starch is too small to be estimated, and when experimenting with adult *Convoluta* it is not until after eight days, in minute green specimens not until after five days, that the starch has entirely disappeared. The leaves of an ordinary plant lose their starch when kept in the dark for a day or two. The demands of the colourless parts are met by translocation of sugar. In *Convoluta* the demands of the colourless tissues are extremely modest; for it is not unreasonable to suppose that the needs of the green cells themselves would account for the slow disappearance of starch from them. The presence of brown masses of digested green cells in such dark-kept adult *Convoluta*, and the avidity with which they and the minute specimens take up artificial substances, is an indication that the nutrition of the animal is affected but slightly, if at all, by the absorption of plastic material from the green cells.

The conclusion, then, seems justifiable that the living green cells purvey little, if any, nourishment to the animal at any stage of its development, and that the association between the green cells and *Convoluta* is best represented as being a form of parasitism. During the earlier stages of the life of *Convoluta* it is the assimilating tissue which is parasitic upon the animal; during the later ones it is the animal which is parasitic upon the assimilating tissue.

3. Photosynthesis.

It is doubtful how far the starch formed by the green cells of *Convoluta* may be translocated from them and used by the animal cells; but there is no doubt that starch is manufactured, and that in considerable quantities. Haberlandt, in experimenting with animals sent from Roscoff to Gratz, notes that the amount of starch contained in the green cells is but

small, and infers that these green cells continually contribute the major part of the photosynthetic process to the animal; but as a matter of fact the poverty of starch must have been due to poorness of condition, for, in their natural state, *Convoluta* always give an intense blue iodine reaction.

We have examined the effect of different rays of the spectrum upon the manufacture of starch by the use of coloured screens placed over animals kept so long in the dark as to be free from starch. We find that when such depleted animals are exposed to light, starch makes its appearance in less than ten minutes in bright sunlight, and that it may be recognised in animals kept beneath screens transmitting red and blue light, but not in animals kept beneath green screens. The appendix and its explanation (p. 377) give the details of the experiment, the main result of which was the following:

After six hours' exposure, the *Convoluta* beneath the red screen, transmitting a band of red light from B to a little beyond C (Fraunhofer lines), showed plenty of starch. The *Convoluta* beneath the blue screen (which transmits a little green light and all the blue) showed a fair amount of starch. Those beneath the green screen (which transmits all the green and a narrow band of extreme red beyond Fraunhofer line B) showed no starch. Naturally this method does not measure the amount of assimilation, but only exhibits the amount of photosynthesised material stored as starch. Yet the results show strikingly that the relative influences of monochromatic light on photosynthesis of the green cells of *Convoluta* are similar to their action on assimilation in ordinary green plants. The maximum assimilation, as indicated by the maximum storage of starch, coincides in both with the light between B and C of the spectrum (λ 660—680). A second maximum, singularly well marked in *Convoluta*, and also known to exist in the case of green plants, occurs in the blue. A point worthy of note is the non-appearance of starch in *Convoluta* under green light. In ordinary green plants green is the region where photosynthesis is the least

active. In *Convoluta* it is so inactive that no surplus of carbohydrate is stored as starch.

It is also noteworthy that the starch-formation in the blue region is in *Convoluta* very considerable, more so apparently than in green plants (see Pfeffer, 1900, p. 390). We may draw a further conclusion from these facts, namely, that the infecting organism—if infecting organism there be—is a member of the Chlorophyceæ (green algæ), and not of the Cyanophyceæ (blue-green algæ), since in the former group the assimilatory maximum is as in *Convoluta*, between B and C, whereas in the latter group it is between C and D (in the yellow). (Pfeffer, 1902, vol. i, p. 344.)

The spectrum of an extract of *Convoluta* chlorophyll shows, even when examined by a hand-spectroscope, the absorption band most characteristic of chlorophyll (between B and C Fraunhofer lines), as well as the absorption at the blue end from about midway between E and F. Faint indications of the other bands characteristic of chlorophyll at the red end of the spectrum were observed. There can, therefore, be no question but that the pigment of *Convoluta* contains chlorophyll. Moreover, as is the case with ordinary green chromatophores of plants, the chlorophyll of *Convoluta* occurs side by side with carotin, which latter substance may be detected by the usual tests—for example, by the bright blue colour resulting from the addition of concentrated sulphuric acid to the dried tissues.

4. Appendix.—Assimilation of Starch by *Convoluta roscoffensis* in White and Monochromatic Light.

In the first experiment young *Convoluta* 1 mm. long were used. They were collected on the shore August 27th, and put in darkness to deplete (August 28th). On September 2nd they were found to be starch-free, and were then placed in glass vessels under screens, transmitting light as follows:—Red screen (a selected piece of ruby glass) transmits from B almost to D (Fraunhofer lines; 0·5—2·5 of Browning's direct

spectroscope scale). The green screens were made (1) of three layers of Baker's green gelatine, which transmits green and a trace of extreme red 0—0·5; (2) of a double glass cell, one compartment of which contained ammoniated copper sulphate, the other potassium bichromate of such strengths as to transmit only green and a narrow band of extreme red 0—0·5. The blue screen contained ammoniated copper sulphate, which transmits some green and all the blue violet. The experiment was made in the open.

Experiment I. — Started 12 a.m. September 2nd.
Recorded 2 p.m.

Red Screen.—All gave starch reaction.

Green-blue screen.—All gave starch reaction.

Red-green screen.—All gave starch reaction.

White light.—All gave starch reaction.

Control in darkness.—All gave no starch reaction.

Experiment II.—For this purpose adult *Convoluta* were used. They had been kept in the dark from August 20th to September 2nd, and had become completely free from starch. The same screens were used as for Experiment I. Experiment lasted from 10 to 12 a.m. September 3rd. The vessels were placed in the open. Direct sunlight was used.

1. Under red screen.—Considerable amount of starch.

2. Under green screen.—No starch.

3. Under K_2CrO_4 screen (= red to green).—Much starch.

4. Under blue screen.—Fair amount.

5. Under white light.—Much starch.

Slight starch reaction obtained after five minutes' exposure to bright sun, and a very distinct reaction after fifteen minutes' exposure to diffuse light.

Section III.—THE DEVELOPMENT OF THE GREEN CELLS.

1. The Occurrence and Significance of Chlorophyll in Animals.

Chlorophyll is known to occur in animals under three distinct forms: (1) as the chromatophores of the green

corpuscles and yellow cells (zoochlorellæ and zooxanthellæ) of Protozoa, Cœlenterates, Turbellaria, etc.; (2) as pigment in the digestive gland (enterochlorophyll) of Crustacea and Mollusca (MacMunn, etc.), and in the gut, blood, fat, skin, and eggs of Lepidopterous larvæ and pupæ (Poulton); (3) as diffused pigment in *Vorticella campanula* (Engelmann, 1883).

Research has shown (1) that some zooxanthellæ and zoochlorellæ are intrusive algal cells, and has rendered the same conclusion probable for some other cases; (2) that enterochlorophyll is a pigment derived from the food (Dastre and Floresco, 1898, 1899; Poulton, 1893); (3) that the chlorophyll of *Vorticella campanula* is probably formed by the animal (Engelmann, 1883). Decisive proof of the formation of true chlorophyll by animals does not exist, but the discovery by Schunck, Marchlewski and Neucki (1901) that chlorophyll and hæmoglobin are closely allied substances removes any *à priori* difficulty in accepting such proof.

The view that the green corpuscles of *Hydra* and *Spongilla* are not cells, but chloroplasts belonging to these animals, has been supported by Prof. Ray Lankester (1881, 1882). "There is no more and no less evidence for considering the green corpuscles of *Hydra viridis* as parasitic algæ than there is for taking a similar view with regard to the green corpuscles of an ordinary green plant" (Lankester, 1882, p. 88). In support of this view, Prof. Lankester asserts the absence of a nucleus and of a cell-wall in the green corpuscles, and the presence of angular colourless and brown corpuscles, which he regards as stages in the development of the green ones.

Since Prof. Lankester's papers on this subject, no really convincing histological proof of the presence of a nucleus, no experimental proof of a cellulose wall, have so far as we know been adduced. Even Beyerinck's paper (1890) gives no figures of the nucleus. Nevertheless there is good ground for believing that these green corpuscles are a phase in the life-history of *Chlorella vulgaris*, since Beyerinck has

succeeded in obtaining cultures of the algæ from the green corpuscles of *Hydra viridis*, and has taken precautions to prevent the infection of these cultures by algæ from without.

In this paper the first form of chlorophyll alone concerns us, and we may briefly consider the evidence for the algal nature of green and yellow cells, and the part they are supposed to play in the animal's economy. The evidence for their algal nature is of three kinds—histological, physiological, and developmental. As regards structure, Brandt and others have shown that many yellow cells and some green ones possess characteristic algal features: an eccentric nucleus; a cellulose wall; a chromatophore, containing chlorophyll and frequently a superficial brown or red pigment; a pyrenoid; an eye-spot (*Zooxanthella conductrix*, Famintzin, 1891), starch, and other inclusions; a biciliate swarm-spore stage (in *Collozoum*, Brandt, 1883). The physiological evidence is afforded by the work of Geddes, Brandt, and others. These authors have shown that the chlorophyll of these green and yellow cells photosynthesises carbohydrate in the presence of light with concomitant evolution of oxygen, and that the surplus assimilate is stored as starch. Lastly, the developmental evidence which is due to Brandt (1883) showed that certain anemones infested by brown cells discharged these cells if placed in darkness. He then put such depleted specimens in filtered and in unfiltered sea water, and showed that the brown cells did not develop in the former, but appeared in a few hours in the latter. Evidence of a slightly different kind has been adduced for the green cells of *Hydra*, of *Paramecium*, and of *Stentor*, by Beyerinck (1890, p. 745, Note 1, and p. 784) and Famintzin (1889, 1891) respectively. These authors made cultures of the cells in various media, and obtained stages identical with those of the common fresh-water alga, *Chlorella vulgaris*.

The proof of the algal nature of these zoochlorellæ and zooxanthellæ is fairly complete. The part they play in the animal economy is, however, far from clear. The most widely accepted hypothesis is the one associated with the term

"symbiosis." According to this hypothesis, the animal draws upon the reserves of the alga, whilst at the same time providing the alga with an environment suitable for renewing the reserves. Direct evidence of such translocation of food material from alga to animal does not exist, and even the experimental and indirect evidence is not satisfactory. Such evidence as we possess is due to Brandt and Geddes. Brandt (1883) experimented with *Sagartia* and *Aiptasia*, and found that when all external sources of food were cut off, those anemones that possessed yellow cells retained their shape and size better than anemones depleted of their cells. Geddes (1879 B) found that dark-kept and therefore presumably starch-depleted *Convoluta roscoffensis* died in a day or two, but that isolated specimens lived for weeks apparently without ingesting food. Finally, Brandt found free starch in certain *Radiolaria*, and concluded that it had passed from the yellow cells.

These experiments and observations do not afford proof of translocation of the algal reserves to the animal tissues, and Famintzin has shown that the evidence points to digestion of the algal cells. He has repeated Brandt's observations, and finds all stages of decolorisation and dissolution of the yellow cells in *Radiolaria* and *Anemones*, and of the green cells in *Stentor* (1889, 1891); whilst Beyerinck (1890) has shown the same to be true for *Hydra viridis*, thus explaining, as it seems to us, the presence of irregular decolorised fragments seen by Lankester (1882). The relationship of alga and animal is therefore to be regarded not as a mutual exchange of complementary advantages (symbiosis). The evidence so far accumulated shows that the alga is a parasite liable at any time to absorption and digestion.

We may therefore summarise the work on zooxanthellæ and zoochlorellæ by saying that in *Hydra*, *Stentor*, and certain anemones these coloured bodies are immigrant algæ or stages of algæ which, if they subserve any function in the animal economy, can at present only be considered as an accessory source of food, available not so much by

translocation of their stored reserves as by digestion of the entire algal cell. From this summary it will be clear that the prevalent opinion as to the algal nature of other green and yellow cells is an inference from these few well-established cases.

2. Views of Previous Writers on the Green Cells of *Convoluta*.

Among the many green cells that have not been critically examined, those of *Convoluta roscoffensis* occupy an exceptionally interesting position; for whereas these green cells resemble Protococcaceous algæ in their chloroplast, pyrenoid, and photosynthetic powers, they differ from all true algæ and resemble animal cells in their lack of a cellulose wall and in their supposed inability to survive the death of the *Convoluta*, or to live when isolated in a hanging drop (Haberlandt, 1891). Experiment, and experiment alone, can decide their true nature.

Up to the present time no rigid experiments have been made. Nevertheless Haberlandt has elaborated an ingenious hypothesis with a view of meeting the exigencies of the case, and Georgevitch has propounded a perfectly distinct suggestion on the basis of a few hatching experiments.

Haberlandt's hypothesis is evidently based on the analogy of chloroplast transmission in the development of plants. The green cells of *Convoluta* are, he suggests, part and parcel of the tissues of this animal, and develop from pre-existing green cells of the previous generation. But this has not always been so. Originally the green cells were independent algæ (as chloroplasts of plant cells have also been supposed to be by Schimper, quoted by Haberlandt, 1891), and their present lack of cell-wall and their inability to lead an independent life are the result of their association with *Convoluta*. Concomitantly *Convoluta* has given up its active and carnivorous mode of life, and now depends on the green cells for its nutrition just as they depend on *Convoluta* for their very existence.

The suggestion made by Georgevitch is based on the result of hatching *Convoluta* in filtered sea water as contrasted with rearing it in water containing the parent forms. In the first case the young hatch and die within two days, during which time they remain colourless. In the second they survive and become rapidly green. Georgevitch concluded that the just-hatched young became infected by green cells from the water containing the parents.

In the following section we show that there is no such hereditary transmission of green cells as Haberlandt postulated, nor is there an infection of *Convoluta* by green cells, as Georgevitch concluded.

Since the structure of the green cells does not allow a precise statement of their animal or vegetable nature, proof must be sought in their development. It might be thought no difficult matter to determine this point by rearing the eggs in sterilised water. The sequel, however, makes it clear that no experiment made with a view of settling the nature of the green cells can be considered valid if the egg-capsule is introduced—a conclusion which we have arrived at only after many laborious experiments. In fact, to obtain eggs or larvæ and to place them in experimental vessels in such a way as to satisfy the demands of the most rigorous criticism that no infecting organism is thereby introduced, is an exceptionally hard task. Yet, unless this difficulty is overcome, the problem of the nature of the green cells cannot be finally decided.

3. The Origin of the Green Cells.

At the time of hatching, *Convoluta roscoffensis* has no green cells, no colourless cells that can be interpreted as a stage in the development of such green cells, and no leucoplasts.

We have satisfied ourselves by repeated observation that no green cells are present at hatching. That no colourless antecedents occur in the just-hatched animal, follows both

from direct observation guided by a knowledge of the form and appearance of the colourless elements that are found in normal *Convoluta* at a later stage, and also from experiments given below. That leucoplasts are absent is a deduction from our experiments made with filtered and sterilised water, which showed that the development of cells with leucoplasts or chloroplasts is not a constant feature of the early life of *Convoluta*, however bright the light may be; whereas, if leucoplasts were present in the egg and followed a course of development such as occurs in plants, their division and metamorphosis into chloroplasts would, in *Convoluta* as in plants, be a constant phenomenon in light cultures. We show that it is possible to maintain *Convoluta* for weeks after hatching, and to expose it for the greater part of each day to direct sunlight, without any indication of chloroplasts arising with them. The development of green cells in certain cultures, their inconstancy in others, and their absence from still other experimental animals, prove that there is no constant development of green cells in *Convoluta* from leucoplasts. We conclude that up to the time of hatching *Convoluta* is devoid of any trace of its future assimilating tissue.

There is no habitual infection of *Convoluta* by a green cell. The green cell develops from a colourless cell. We have seen two such translucent cells the day after hatching, but the time of their appearance varies very greatly. They lie in the central syncytium or gut, surrounded by one or more nucleated wandering cells, and it is probable that from whatever source they were derived fresh supplies may accrue.

We have observed the transformation of colourless into green cells two days after hatching, a result obtained by subjecting the larval *Convoluta* to several hours' direct sunlight. If diffused light is employed, the change of colour occupies a much greater length of time (from one to two weeks). Once the change is effected, multiplication of the green cells proceeds apace. The change of colour is accompanied by a change of site. The colourless cells occur in

the "gut," the green cells in the peripheral parenchyma, which is their definitive station.

This change, however, does not immediately affect all the colourless cells. A certain number remain unaltered, moving towards the hinder end of the body. Immature *Convoluta*, .74 mm. in length, contain posteriorly placed colourless cells, and some may be found in this position even in adult specimens. New supplies of green cells may arise from these colourless elements as well as by division of already pigmented cells. Hence it follows that a knowledge of the origin and development of these colourless cells is the key to the problem of the green cells (see Pl. 31, figs. 19, 20).

The most feasible way of attaining a knowledge of the real problem and its solution appeared to be to experiment with *Convoluta* on the supposition that the colourless cells must be either intrinsic or extrinsic. We have seen that, at hatching, the larva is free from any trace of these cells or their future contents. By allowing such larvæ to develop in sterilised water, the problem of infection or non-infection could, we thought, be solved.

Accordingly we prepared vessels filled with ordinary sea water, sea water sterilised at 60° C. and 80° C., and filtered through a Pasteur-Chamberland filter. In some of the vessels, ordinary water free from *Convoluta*, but rich in diatoms, was given as food; in others sterilised sand; and, again, in others no food was introduced. At first we employed egg-capsules; afterwards just-hatched larvæ were placed in the vessels. During the experiment we subjected the animals to various light conditions. Equivalent lots were kept in diffuse light, in darkness, and in bright daylight.

The results of this first series of experiments showed great irregularity in the appearance of colourless cells; but colourless cells appeared in some animals of all the cultures—whether in unfiltered, filtered, or sterilised water; whether in light or darkness; and whether with sand or without. Not only did colourless cells appear in isolated larvæ or in larvæ of a batch reared from the capsule, but when exposed to bright light

they became green in the sterilised as well as in the non-sterilised or filtered cultures. Thus, whilst the occurrence of these colourless cells was such as to preclude their development being considered a normal one associated with the presence of pre-existing leucoplasts, their presence in all the cultures, and their metamorphosis into green cells, seemed to afford proof of their internal origin. We concluded that they were intrinsic structures.

Feeling, however, that such a conclusion could only be adopted after confirmatory experiments made with every precaution, we prepared another series of cultures, and in doing so lighted upon a serious source of error, which showed us that not only is every experiment made with sterilised water, into which the egg-capsule of *Convoluta* is introduced, worthless, but that extraordinary precautions have to be taken to avoid contamination when introducing larval *Convoluta* into the experimental vessels.

The source of error lay in the cells that adhere to the egg-capsule. During the act of egg-discharge and capsule-formation the tissues of the parent undergo violent disruption. Frequently the body breaks in two across the opening of the oviduct; not infrequently the hinder half remains attached to the capsule, and there disintegrates. But invariably a discharge occurs of cells that adhere too firmly to the capsule to be washed away. A few days after ovulation the surface of the capsule is covered with other elements, which have the appearance of the growing and dividing cells of an alga in the *Palmella* stage. Thus we find masses of very pale greenish cells (fig. 3) and linear colonies of colourless elements, some with thick walls and refringent contents, others with no apparent wall and clear contents (fig. 3, *C—G*). Again, we find linear bifurcating green filaments, evidently the vegetative thallus of an alga, and recalling the filamentous form of the polymorphic *Proto-coccus* (see Chodat, 1902). There is ground for believing that these growing and actively dividing organisms are derived in some way from the body of *Convoluta roscoff-*

ensis, but we have not been able to undertake pure cultures of its green cells or of its persistent colourless cells with a view of proving the origin of this capsular flora from the disjecta of the parent. The ground for the belief lies in the fact that every important kind of capsular cell (except the filamentous ones) can be matched by cells in *Convoluta* itself. Experimental proof, however, is needed, since a great exotic fauna and flora of algæ, diatoms, and Protozoa also occur on the capsule. The amount of contamination adhering to the capsule varies considerably, but we have not seen a single case of a capsule free from some one or other of these remarkable cells.

It will now be clear that the constant presence of these contaminating tissues is a source of error which precludes the use of egg-capsules in any experiment with sterile water on the nature of the green cells and their colourless predecessors in *Convoluta*. That precautions of no ordinary kind have to be taken in isolating larvæ and transferring them into jars of sterilised water, also follows; for these larvæ, even before escaping from the capsule, may ingest some of the colourless capsular cells, or some of the latter may be transferred with the larvæ by the action of the pipette.

To obviate these sources of error is a matter of the greatest difficulty, which, indeed, we cannot claim to have completely overcome. But experiments in this direction—such, for example, as seizing *Convoluta* at the moment of hatching, and washing them several times in sterile water before transferring them to other sterile water—all point to the conclusion that the more precautions of this kind are taken, the fewer colourless antecedents of green cells are registered in larvæ reared in sterilised or filtered water.

These precautions were taken in our last experiments. Advanced embryos as well as larvæ were taken out of the capsule, and carefully and repeatedly and appropriately washed before being placed in the normal, filtered, or sterilised sea water. Control cultures were arranged so that access to the

capsule was possible. Bright light, diffuse light, and darkness were employed. No sand was introduced, as we found that the reserves afforded quite sufficient nourishment to enable the *Convoluta* to live and develop for a couple of weeks.

The experiment was begun on September 9th, and lasted till September 21st. The results showed the value of the precautions. Those cultures which had been made by subjecting isolated embryos or larvæ to filtered water showed no trace of colourless cells, although several dozens of such isolated specimens were employed. The cultures in water sterilised at 60° C. and at 80° C. showed but three cases of colourless cells in between thirty and forty larvæ, all of which had grown and developed and were active at the time of closing the experiment. Sterilised cultures in which the egg-capsule had been inserted showed a much higher percentage of the occurrence of colourless cells. In ordinary sea-water cultures, both with or without capsules, colourless cells were almost invariably present. These results point very decidedly to the capsule or sea water as the source of the colourless cells.

3A. Conclusions on the Origin of the Green Cells.

We may now sum up the evidence we have obtained as to the origin of the green cells of *Convoluta*. There is no habitual infection of *Convoluta* by a green cell. The future assimilating tissue consists at first of colourless cells. No trace of either green or colourless cells or of plastids has been found before the time of hatching.

The evidence gained by isolating embryos and larvæ in sterilised and filtered water goes to show that the more care is exercised in preventing contamination from the capsule, the fewer cases of colourless cells are subsequently registered. Access to the capsule and the use of ordinary sea water favour the appearance of colourless cells. It is therefore probable that the colourless cells infect the larval *Convoluta*

from without. Indeed, the capsular fauna contains numbers of colourless cells similar to those which constitute the first stage of the assimilating tissue.

The evidence of the first appearance of the colourless cells, their position in the gut, and their structure, as detailed in the next section, are also in favour of the infection hypothesis. They appear most constantly in cultures made from the capsules, but even in these a certain capriciousness is very obvious. Larvæ from the same clutch rarely contain colourless cells to the same number, or in the same stage of development. Some have several, some few, some none at all. This irregularity of appearance and occurrence under apparently identical conditions is a strong argument against the colourless cells being normal intrinsic developments of the animal tissues, and also against a plastid theory of the origin of the chloroplasts independently of the cells in which they are subsequently found; but it is readily intelligible if infection occurs now rapidly after birth, now only after an interval of some days, and it may be not at all.

The position of the colourless cells in the gut enclosed by wandering cells, in contrast to their definitive position in the more superficial parenchyma, is also in favour of the infection theory, since we have seen that wandering cells carry food thither. Finally, the structure of the colourless cells, as given in the next section; the changes which they undergo during their conversion into assimilating green cells; the gradual enclosure of the colourless cytoplasm by one or more chloroplasts which pass through a colourless or yellowish phase, and finally adopt a green tint; the occasional presence of starch in the leucoplast stage; the presence of a coloured eye-spot or stigma; the gradual development, in most cases, of the power of photosynthesis, are phenomena all of which occur in plants, and can be closely paralleled in certain algæ, which, after a period of saprophytic life, during which they have lost their chlorophyll and stored up reserves, enter upon a period of ordinary holophytic nutrition (Cohn, 1864; Kruger, 1894; Karsten, 1901; Dangeard, 1902).

Nevertheless the phenomena of the green and colourless cells of *Convoluta* are, so far as we know, not collectively found in any known algæ. The absence of the cellulose coat, for example, is, we believe, unique. Yet the knowledge of the influence of saprophytic and parasitic life upon the structure and development of algæ is so scanty (Grintzesco, 1903) that we can but hope that, when more complete investigations have been made, light will be thrown on the nature of these green cells of *Convoluta*. We conclude this section by pointing out how the present research may give points of departure for such work.

We have seen that Haberlandt isolated green cells, maintained them in a hanging drop, and found that under these conditions they ceased to divide and gradually disintegrated, whence he concluded that apart from *Convoluta* the green cells are incapable of existence. It is, however, clear from the foregoing description (see also p. 53) that, when discharged during oviposition, the green cells find themselves attached to a mucilaginous capsule and surrounded by a richly proteid substance. Under these circumstances their fate may be a very different one from that which overtakes green cells isolated in sea water. Hence Haberlandt's conclusion is only true for the conditions of his experiment, and it is quite possible that the green cells are but one phase in the life-history, or one of the forms of vegetative growth of a polymorphic organism (cf. Chodat, 1902).

4. The Development of the Green Cells from Colourless Predecessors.

The researches of Geddes, von Graff, and especially of Haberlandt, have elucidated the chief features of the green cells. Thus it is known that they form a single layer in the outer parenchymatous zone, and that they consist of a naked spherical or pyriform protoplast, containing a usually single chloroplast, a pyrenoid, and an excentrically placed nucleus. Besides the rod-like masses of starch, varying amounts of a

granular substance, soluble in distilled water, but insoluble in absolute alcohol, occur round the nucleus.

We have now to trace the development of these green cells from their colourless predecessors. In doing this it is necessary to consider the latter in more detail than in the last section. We therefore begin our description with the appearance of the colourless cells of the recently hatched *Convoluta*.

The simplest form of colourless cell is spherical, measuring $\cdot 006$ — $\cdot 01$ mm. in diameter, and consists of a clear substance and delicate wall, which does not give a cellulose reaction. In fact, such cells resemble nothing so much as a vacuole with a refractive enclosing membrane. More usually within the "vacuole" there are one or more inclusions of a highly refringent character. Sometimes the inclusions are divisible into several marginal ones pressed against the membrane, and one or more central bodies (Pl. 31, fig. 14). More usually irregular, curved, more or less comma-shaped inclusions occur massed together at one pole of the cell (Pl. 31, fig. 12, *Chr.*); and again, a mass of fine but highly refringent spherical granules may take their place. The occurrence of starch is no less inconstant than the form of the inclusions. In some cases (Pl. 31, fig. 8) starch can be detected with the utmost clearness in each of the marginal and central bodies, though these have as yet no colour. In such cases true leucoplasts, with an amount of carotin too slight to cause recognisable coloration, must be present. In the majority of cases, however, no starch can be detected by the most careful manipulation of the iodine reagents. It is therefore doubtful whether the irregular inclusions are leucoplasts devoid of starch or are protein crystals.

The development of the chloroplasts is, again, a variable one. In those cases in which marginal starch-holding leucoplasts are present, a yellow pigment appears in each. In other cases a green envelope gradually encloses the inclusions. The latter is certainly the more usual method. Long after the single chloroplast has acquired its full green colour the

inclusions are visible. It is therefore probable that they act as reserve materials. The figures 8, 12, 13, and 19 illustrate the changes which accompany the formation of the green cells from colourless ones.

In addition to the structures we have mentioned, the occurrence of a curved crimson band, an eye-spot, or "stigma," is noteworthy, and has only previously been observed by Famintzin in the green cells of *Stentor*. It is placed on the surface of the colourless cells, and persists for a long time after the green colour is established (Pl. 31, figs. 8 *C*, 19 *B*, 20). This little stigma, so similar to the organ of Volvocineæ and many other Chlorophyceæ, and so utterly unknown in animal tissue cells, is in itself almost sufficient to establish the immigrant character of the colourless and green cells.

5. The Influence of Light.

The first appearance of chlorophyll in the colourless cells is influenced to a remarkable extent by the conditions of illumination, though, when once fully established, it is extremely stable, and in the majority of chloroplasts is but little affected by continued darkness or dim light. A very bright light (direct sun) is required to quickly effect the production of chlorophyll in such amount as to be noticeable to the eye under high microscopic powers. The change may then be produced in twenty-four hours. Otherwise, in diffuse light, sufficient chlorophyll may not appear in the colourless cells to produce a green effect even after a fortnight. Like every other feature in the development of the green cells, the influence of light is variable; some *Convoluta* become rapidly green in diffuse light, and others, to all appearances as favourably situated, remain colourless. The explanation of this variability appears to be that *Convoluta* makes a pure culture from a mixed infection. The infecting organism is ingested in all stages, and some of these stages develop less readily into the green-cell condition than do others.

It is, indeed, known that one and the same alga exhibits

much variation in the form of its chloroplasts and inclusions. Changes in the chloroplasts of diatoms and Flagellata, for example, accompany a change from holophytic to saprophytic existence (Matruchot and Molliard, 1900; Karsten, 1902; Dangeard, 1902). Hence the irregularities in the development of the colourless cells to the green cells within the body of *Convoluta* cease, with deeper insight into the complexity of the process, to be a matter of surprise.

The influence of prolonged darkness on the colourless cells remains to be considered. We have seen that in darkness, as in light, these elements may make their appearance in larval *Convoluta*. In light a more or less gradual development of chlorophyll takes place. In darkness this is not the case, though, as we have just mentioned, chlorophyll once well established is not destroyed by absence of light.

A number of young *Convoluta* were reared from the capsule in sea water with their parents, and, after acquiring a supply of colourless cells and a few green cells, were transferred to jars of sea water placed in darkness. The transfer was made on August 24th, the *Convoluta* being then two to three days old. On September 4th—that is, after an interval of eleven days—they were examined. Some contained several green cells. In others the green colour was replaced by yellow diffuse pigment, and in these cases numerous irregular inclusions and fine fatty granules were also present. In these latter cases the yellow chlorophyll occupied only a small portion of the periphery of the cell. In yet other examples the contents of the cells were composed of yellowish globules and of finely divided fat. These specimens form a series (see fig. 6 A) leading from typical green cells to mere aggregates of fat staining deeply with osmic acid. There can be no doubt that in this case we see the degeneration of the chromatophores under the influence of darkness combined with starvation.

Having shown that high light-intensity favours the development of chlorophyll in the colourless cells, and that darkness with, presumably, concomitant starvation causes degeneration

of chlorophyll in the developing green cells, we attempted to investigate the action of monochromatic light. For this purpose larvæ from the vessel A used in the preceding experiment were employed. They were placed under screens transmitting red, green, and blue light respectively. The result of three successive days' exposure to filtered sunlight showed that the colourless cells of the larvæ were the most developed in green light, agreeing with those exposed to white light; those in the blue light had remained stationary; and those in the red light were in an intermediate condition. None of these cells had become green, whereas larvæ hatched from comparable batches of eggs placed in the light had in the same interval of time become distinctly green.

We conclude that a high light-intensity is favourable, and that darkness is inimical, to the formation of chlorophyll in developing green cells. But inasmuch as the infecting organism when ingested is now at one stage and now at another stage of development, the influence of light is not regular. It may call forth the development of chlorophyll with extraordinary rapidity, or it may induce it but very slowly.

Section IV.—THE TROPISMS OF CONVOLUTA.

Geddes has shown that *Convoluta* is positively phototropic. Left to themselves in a jar of water laterally illuminated, the animals mass themselves up on the brighter side. Haberlandt has demonstrated that the rising up of *Convoluta* to the surface of sand or water, which occurs when the containing vessel is perfectly still, is a negative geotropism, and not a movement toward oxygen. He also showed that extremely slight vibration is sufficient to inhibit the negative geotropic reaction, and to cause the animals to collect at the bottom of the vessel in which they are kept.

The object of this paper, the investigation of the bionomics of *Convoluta*, required of us to examine somewhat more closely into these tropisms in order that we might discover

the parts played by them in determining the habits of the animal.

1. Geotropism.

The young *Convoluta*, the moment after hatching, reacts to gravity like the adult. In a perfectly still vessel *Convoluta* is negatively geotropic: it rises to the surface of the water. Indeed, the active revolution of the unbatched animal, whilst closely invested by the egg-membrane, may be of the nature of a geotropic response, persistent because ineffectual. We make use of the negative geotropism of the larvæ in collecting them for experiments.

The downward movement called forth by vibration takes place both in adult and larval *Convoluta*, but by different methods. The adult generally releases its hold and allows itself to fall to the bottom of the vessel,—sometimes, however, gliding vertically downwards along the vessel's wall. The larvæ turn head downwards and swim in a descending spiral to the bottom.

The positive geotropism of *Convoluta* is associated with the presence of an otocyst. The statical and equilibrating functions of this organ have been the subject of much recent research, but the influence which it exercises on geotropic response has, we believe, not been determined. That the otolith plays such a part is clear from the fact that occasional larvæ of *Convoluta* do not exhibit the usual positive geotropism when stimulated by vibration. In such cases examination has shown that the otolith was missing, a feature occurring sporadically even in embryos developed from the same clutch of eggs.

Though the geotropic movement of old and young *Convoluta* are among the most striking movements which they exhibit, there are nevertheless times when the animals, young and old, are refractory to the stimulus of gravity. Thus every day the animals pass, late in the afternoon, into a singular lethargic state. In this condition, observable alike in the open and in the laboratory, the animals lie in inert masses, sticking to one

another by the viscid excretion with which their surfaces are covered. Whilst thus, they refuse altogether to react when the water in which they lie is agitated. Green lumps of cohering thousands are often broken off from such masses and carried seaward by a water current running down the beach (cf. Pearl, 1903).

The power of reaction to gravity resides in the anterior end of the animal. If *Convoluta* is divided by a transverse section into a "head" end and a "tail" end, the head end rises; the tail end, although capable of active swimming movements, remains at the bottom in still water. The tail end falls when placed at the surface of the water; the head end remains there unless the water is agitated, when their reaction to gravity reverses its sign and they fall.

Animals subjected to prolonged darkness, or dim light, exhibit negatively geotropic movements in a constantly increasing measure. To such an extent may the reaction to the stimulus become developed, that animals contained in a funnel lined with filter-paper and kept half filled with water may crawl up the paper beyond the surface of the water and be ultimately dried up at the top. Since *Convoluta* possess a great power of resisting desiccation, the animals to die thus must have maintained themselves for days in this unwonted position. This is only one of several instances we mention which show that these tropisms are hard taskmasters. The lethargic condition in particular is interesting, and suggests the interpretation that the modifications of habit which are favourable to the photosynthetic function of the green cells are apt to be embarrassing and even dangerous to the animal itself.

2. Thermotropism.

We deal next with the reaction of *Convoluta* to change of temperature—a reaction which is less marked than that due to light or gravity, and has not been noticed by Haberlandt or other observers. If *Convolutas*, uniformly illuminated, are placed in a trough containing water, the animals spread

themselves evenly throughout the trough. If the temperature of the water at one end of the trough is gradually raised from 18°C. to 30°C., no thermotropic movement occurs. At 35°C. the animals begin to move toward the cooler end (negative thermotropism). What appears to us to be particularly noteworthy is the fact that a temperature of from 35°C. to 38°C. is fatal to *Convoluta*, and consequently many animals die before they have succeeded in escaping from the heated end. That *Convoluta* is capable of enduring a high temperature is shown by the fact that when the source of heat used in the foregoing experiment is removed, and the water allowed to cool, *Convolutas* which had massed themselves up at the cooler end begin to invade the warmer end whilst the temperature there is still 30°C. This movement may not, however, be a positive thermotropism, but merely the expression of a tendency of masses of *Convoluta* to spread themselves evenly when not prevented from doing so by unilateral light. *Convoluta*, then, is negatively thermotropic only just below its death-point. It manifests attunement to a high heat-intensity.

3. Phototropism.

Previous observers have recorded the positive phototropism of *Convoluta*. We have sought to determine the limits within which this reaction occurs, and the influence which it has upon habit. Positive phototropism is well marked in light of medium intensity, but is not manifested in light of low intensity. For example, it does not occur in a room removed from direct light, although the light therein is high enough to enable observations on the disposition of *Convoluta* to be made. Again, light may induce a negative tropism. Thus a sudden reduction of illumination evokes a sudden, though transitory, "negative" movement. This is well shown in Text-fig. 2, which represents an experiment made for the purpose of determining the specific effects of various parts of the spectrum. Series 2 of these figures

indicates the immediate negative phototropic movement induced by suddenly raising the light-intensity.

Unlike this transitory "negative" effect—of the nature of shock,—the "positive" movement induces a remarkably permanent disposition. The animals remain the whole day long massed up in the brighter side of the vessel, but only so long as the light conditions remain fairly constant. A shadow thrown over them suffices to disturb and to cause them to mass themselves evenly throughout the vessel.

From the above it follows that though phototropism only occurs when the light-intensity is high, yet exceedingly slight differences of intensity serve as stimuli.

As is the case with green plants, external conditions, especially light conditions, exert normally and continually a certain general influence on the condition and state of irritability of *Convoluta* (tonus or paratonus). In both plants and in *Convoluta* the nervous states and metabolic activity is in part the outcome of a constant rain of internal and external stimuli. When we speak of tone, we refer to the modified tone compounded of the autonomous and of the induced tone. This light-induced tone (phototonus) is one of the most striking features of *Convoluta*. When the tonic influence of light is withdrawn—as, for example, by maintaining the animal in darkness for several days—*Convoluta* passes into a sluggish condition. In this state it lies motionless, its muscles contracted so that it becomes shorter and of a darker green colour by reason of the massing together of its green cells. On re-exposure to light this state rapidly passes away. From what we have said previously with respect to the marked negative geotropism of dark-kept *Convoluta*, and from the above observations, it follows that dark-rigor only subvenes gradually, and that phases of dark-rigor are succeeded by progressively shorter periods marked by high irritability to the stimulus of gravity.

We infer from the phenomena presented in dark-kept *Convoluta* that light exerts a constant (phototonic) influence on *Convoluta*. But when the light intensity is

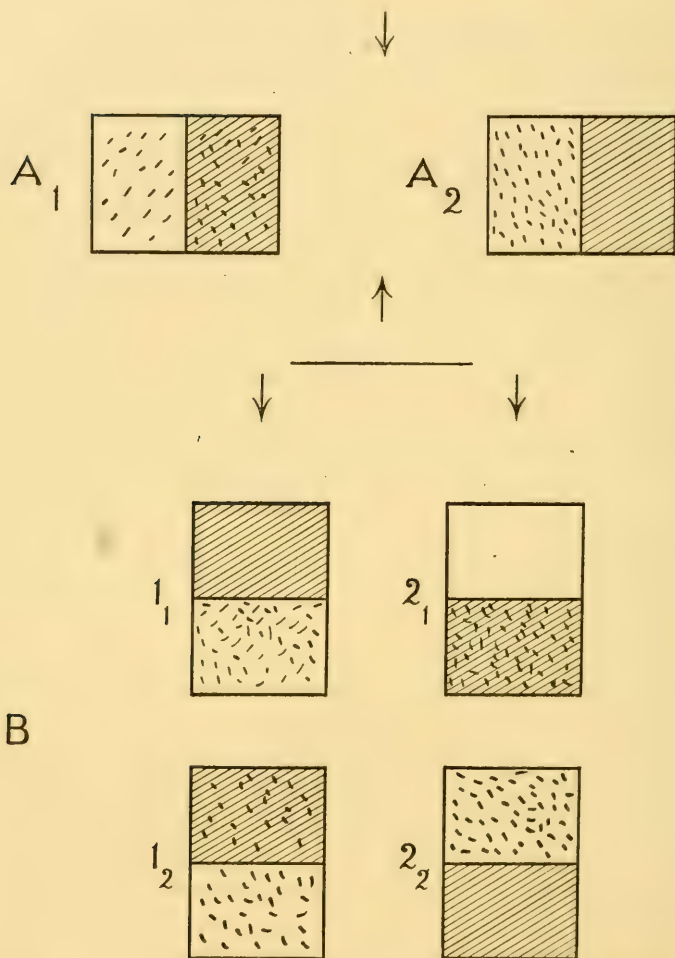
maintained above a certain degree, *Convoluta* passes into a condition of light-rigor—that is, into a state akin to that induced by darkness. At this high light-intensity the phototonic influence of light is withdrawn or greatly disturbed.

Further, we have to distinguish between the constant tonic effect of light, which can only be estimated indirectly by noting the effects of prolonged darkness, and the directive influence of lateral light, which induces phototropic movements. These two modes of influence of light are known to operate among plants, and it is interesting to recognise them at work on *Convoluta*.

Before passing on to describe how another light-factor serves as a stimulus to *Convoluta*, we may mention that prolonged darkness produces no appreciable destruction of the chlorophyll of the mature green cells, nor does it impair their photosynthetic powers. After a fortnight in complete darkness, all starch may disappear from the green cells. Then, exposure to bright light induces starch-formation within five or ten minutes.

We have now to refer to the influence of background on the movements of *Convoluta*, and to show that this light-factor may materially modify the phototropic response. In our work on the physiology of the higher Crustacea we have shown that background plays an important part in determining direction of movements.¹ This is true also of *Convoluta*. To demonstrate the influence of background, we use two shallow porcelain troughs, the bottom of each of which is half black and half white. We add to each trough some fifty *Convoluta* and a little water, distributing the animals evenly over the bottom. If the troughs are so orientated that the two halves are equally illuminated, all the *Convoluta* rapidly pass to the white half. If the troughs are so placed that in one the white half and in the other the black half is the more illuminated, and if equal numbers of *Convoluta* are placed on the half of each distant from the light, then within two minutes the proportion of animals on the white to those on

¹ 1902 (abstract).



TEXT-FIG. 1.—Diagram illustrating the influence of background (white or black) on the movements of *Convoluta roseoffensis*. The animals are placed in shallow porcelain troughs, the bottoms of which are half white and half black (shaded). Each dash represents a *Convoluta*. A. In uniform light. A_1 . At beginning of experiment, *Convoluta* fairly uniformly distributed. A_2 . After forty minutes, *Convoluta* all on white ground. B. In lateral light (arrows show direction of light). Fifty *Convolutas* placed in white half of 1_1 and fifty in black half of 2_1 . 1_2 and 2_2 show the results after two minutes:— in 1_2 ratio on black and white = $\frac{20}{30}$; 2_2 ratio = $\frac{0}{50}$. See text.

the black half is—in the case where white ground is nearest the light, 50:0; in the case where black ground is nearest the light, 30:20.

Thus the background modifies phototropic response; the animals tend to remain on a white ground and to shun a black ground, and to such an extent that when for the execution of a phototropic movement the passage from a white over to a black ground is involved, a large proportion—two thirds—of the animals fail to perform that movement.

Phototropism is, then, not an inevitable reaction. Under certain conditions its sign is reversed; under others it fails to take effect. We give a further illustration of what we feel is an important and general fact, that a “reflex” has something of the uncertainty which attaches to a movement in which volition is concerned, and something of the complex of conditions which in the latter class of actions constitute “choice.”

Periodic Tidal Effect.

If, as the *Convolutas* expose themselves on the sand after the tidal water has withdrawn from above them, a small patch of some thousands is scooped up into a vessel, the animals immediately disappear beneath the sand scooped up with them. As soon as the vessel ceases to be shaken—when laid on the ground in the open, for example—the green patch of *Convoluta* reappears. It persists for some hours, but then melts away again, only to appear once more after a few hours spent below the surface.

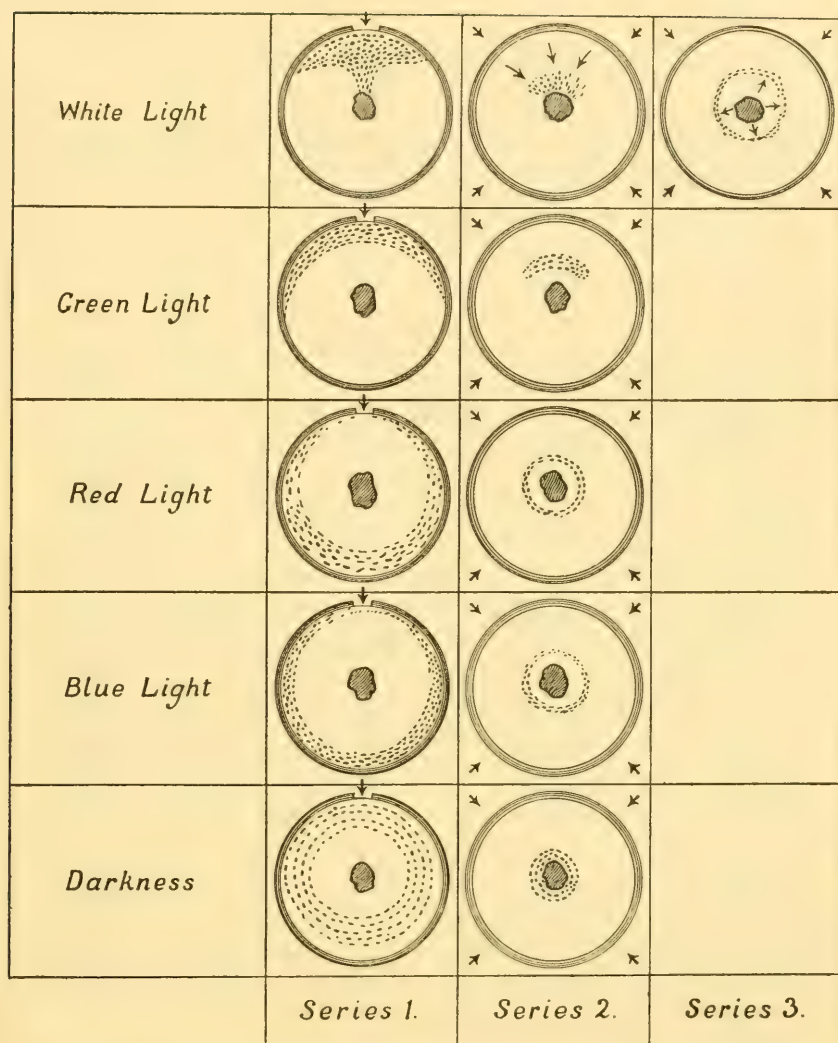
This coming and going, apparently so erratic, is obedient to a simple rule. If, after watching the patch disappear beneath the sand of the vessel, one looks away to the strip of sand whence the animals were taken, one finds that the returning tide is already lapping its edges; and inspection shows that the colonies of *Convoluta* known to inhabit that stretch of sand are all now beneath the surface. If, again, one remarks the time at which the tide

ebbs from that strip of sand and at which the green colonies reappear, and looks again at the vessel containing the sample, it, too, will be found to be covering itself with its green scum of *Convoluta*. *Convoluta* serves for a brief space as a tide-table. It exhibits a periodic vertical movement whose rhythm is that of the tide. The rhythm is not profoundly impressed upon it; after a day the movements of the patch in the vessel cease to synchronise with those in the open. Dark-kept animals show no periodic "tidal" movements. From this we conclude that the descending movement of *Convoluta*, whereby it sinks in the sand just as the tide is reaching it, is due to light. When the summation of light stimuli passes a certain amount—if we may use this figure—the influence of lateral light no longer produces a positive effect. The animal's reaction to gravity becomes changed in sign. It sinks. When the light experience—the after-effect of light stimulation—is dissipated, during its sojourn in darkness, the animal becomes once more negatively geotropic and rises to the surface.

To sum up: within certain limits of light-intensity *Convoluta* is positively phototropic; at a higher intensity it is temporarily negatively tropic. On certain backgrounds it is aphototropic; and at certain periods in its normal habitat it is either aphototropic or more probably negatively phototropic.

4. The Influence of Monochromatic Light on Phototropism.

The phototropisms of plants are chiefly due to the rays of high refrangibility—blue and violet (Pfeffer, 1902, p. 117). It was of interest, therefore, to determine whether the phototropism of *Convoluta* is also due to these rays. Our experiments were made in the following manner:—In each of five very shallow (1 cm. high), circular, porcelain jars a central heap of sand, a little water, and a batch of *Convoluta* were placed. Each of four of these jars was covered by a



TEXT-FIG. 2.—Diagram representing phototropism of *Convoluta roscoffensis*. The circles represent ground-plans of shallow porcelain vessels containing a central heap of sand, a little sea water, and many *Convolutas* (represented by dashes). The break in the circle (Series 1) indicates the position of the window in a blackened bell-jar placed over each porcelain vessel. The arrows outside the circles represent the direction of the light. Series 1 shows the disposition of *Convoluta* at the time of removal of the covers. Series 2 shows the instant negative phototropic reaction set up by removing the covers (raising the light-intensity). Series 3 (only one example shown) shows the recovery (a few seconds after Series 2) of the positive phototropism. The green light was produced by passing daylight through three of Baker's green gelatine films; the red by using three of Baker's red films; the blue by using four of Kirchmann's blue films and one green film. (The blue and green lights were not absolutely monochromatic.)

blackened bell-jar admitting light through a small "window." The windows of these four covering bell-jars admitted respectively white, green, red, and blue light. The windows were made by combinations of gelatine films, so selected as to give, when tested by a hand-spectroscope, approximately monochromatic light. The fifth cover admitted no light.

Text-fig. 2, Series 1, shows the dispositions of *Convoluta* when subjected to these light conditions. As is seen from these figures, white light and green light induce a positive phototropism. Darkness and blue light produce no asymmetry of arrangement; whilst in red light the animals either remain irregularly distributed, or show some indication of negative phototropism. Hence the rays which determine the positive phototropism of *Convoluta* are not those which determine the movements of plants. From this it would seem probable that the phototropic movement of *Convoluta* is independent of any influence which its green cells may bring to bear upon it. It is, however, interesting to note that this utilisation of the green rays makes for economy, for the green rays are just those of which chlorophyll absorbs least, and with which it can most readily dispense. Whether light induces its effect by acting on peripheral nerve-endings, or in the eye-spots of *Convoluta*, we have not determined.

We will conclude our study of phototropism by a brief reference to the behaviour of young and sectioned animals to light. Just as, in animals divided transversely, the head ends only are sensitive to gravity, so are they alone sensitive to light.¹ Inasmuch as oviposition takes place just beneath the surface of the sand, the tail-ends—which may be, as we have already described, torn off in the process—remain below the surface, and, decaying, serve to nourish a rich saprophytic flora.

Though young *Convoluta* are strongly, positively phototropic, the just-hatched larvæ are aphototropic. After a

¹ Loeb (1894 and 1900) refers to a similar result in the case of *Thysanozoon*, and neither this author nor Parker and Burnett (1899) obtained a differential effect with fresh-water planarians.

few hours of free existence they acquire this tropism which becomes such a masterful factor in determining their habits.

5. Reactions to Two or more simultaneously Applied Stimuli.

Convoluta offers admirable material for an investigation into the nature of the reflex movement which occurs when two or more stimuli are combined. As would be expected, one stimulus often dominates another completely, so that the response is that which would occur were the dominating stimulus alone applied. This is illustrated in a striking manner when *Convoluta* is subjected to both heat and light stimulation. To this end we place a shallow, oblong trough with its long axis parallel with the direction of the light. *Convoluta*, placed with sea water in the trough, mass themselves up on the side toward the light. This end of the trough is gradually heated, and though, under ordinary circumstances, *Convoluta* is negatively thermotropic (at about 35° C.), the animals remain in the position induced by light, and die in dense masses as the temperature reaches the fatal point (about 38° C.).

But, in the case of light- and gravitational stimuli acting together, the resulting position shows that each has produced an effect, though the action of the one stimulus modifies that of the other. When, for example, *Convoluta* is placed in a tall glass cylinder with water, the animals rise to the surface and mass themselves on the side toward the light. But if the light-conditions are modified so that the brightest region is some distance below the surface—as, for instance, by interposing a screen consisting of several plates of ground glass or a black card between the source of light and the top of the water,—*Convoluta* at once releases its hold and swims downward to take up its position just below the edge of the glass screen, where the light is brightest. It subordinates its geotropic to its phototropic reaction. If, however, only one ground-glass plate is used, so that the difference

in illumination behind the plate and below it is not great, no reaction occurs. Here the stimulus of gravity dominates that due to light. In the reflex groundwork of nervous activity something akin to the phenomenon of attention in psychic life already exists, just as in the phenomenon of after-effect, especially in that peculiar after-effect which produces rhythm, we have the reflex analogue of psychic memory.

6. Rheotropism, Thigmotropism: Application of the Tropisms.

Beside being influenced by light, gravity, and heat, the movements of *Convoluta* are also conditioned by the strength of the water current and by the nature of the surface on which the animal rests. These influences, as well as those of light, gravity, and heat, we consider in relation to the habits of the animal in the next section.

We will conclude by pointing out in what ways a knowledge of the tropisms above described is useful in the manipulations required in an investigation of *Convoluta*.

To obtain plentiful supplies of eggs, we make use of the positive phototropic reaction. A great number of mature *Convoluta* is collected in a large dish placed opposite a window. The animals move up to the light; at nightfall the dish is turned round. In the morning the animals all cross to the lighted side, and the egg-capsules deposited at night may be picked out free from parents.

Again, young *Convoluta* are only seen with difficulty, owing to their minuteness. We prepare a sheet of white paper and lay on it a black cloth, and so rest the dish containing the young animals that the greater part of it is on the black background. The animals collect on the part of the dish above the white ground. There, however, they are all but invisible, so that the dish must be gently turned till the part previously on the white is on the black ground, against which the animals are easily seen. To transfer a young *Convoluta* from one vessel to another is difficult enough till its geotropism is pressed into service. The animal is lifted

in a pipette, but if the nipple is pressed even gently the water is expelled, and *Convoluta* is left sticking to the side of the glass tube. The pipette must be held vertically and as still as possible. The slight involuntary shaking of the hand suffices to render it negatively geotropic. The animal is allowed to swim down till it reaches the drop of water at the tip of the pipette. The gentlest pressure of the nipple is then sufficient to transfer it to the required vessel.

No attempt should be made to transfer young or old *Convoluta* whilst they are in the lethargic stage (see p. 396). To separate young from old *Convoluta* the animals are allowed to take up their light position in an unequally illuminated dish containing several inches of water. The dish is then tilted slightly on the side where the *Convolutas* are congregated. The old descend more rapidly; and the young, less active, and readily visible against a dark ground, may be secured with a pipette.

Section V.—ECOLOGY.

1. Position of the Colonies of *Convoluta*.

The most striking feature of the distribution of *Convoluta* is its occurrence in vast colonies. We now describe the appearances presented by these colonies at Trégastel, Côtes du Nord, Brittany. The colonies occupy a definite and usually narrow zone high up the beach just below the high-water mark of the neap tides. Usually each colony consists of a number of separate well-defined patches, the appearance of which can be understood from Pl. 30, figs. 1, 2. The shapes and sizes of the patches and the sites they occupy remain, broadly speaking, uniform for months together, though subject, as we shall see, to secular periodic changes. Immediately after the receding tide has uncovered the "Convoluta zone" of the beach, the colonies rise up to the surface of the sand. Each constituent patch takes up a certain position, which may be shifted landwards, but more

often seawards, during the early hours of ebb tide. As a whole, however, the colony remains till the flowing tide is about to cover it—a green inert mass. Then it vanishes in a few minutes, to reappear next day in the same spot.

In the spring, during April, the colonies and their constituent patches increase so rapidly as to completely occupy that belt of the shore which we call the *Convoluta* zone, along which but few patches were previously visible. The number of individuals in an average-sized colony is prodigious. Von Graff (1891) has estimated that 1 c.c. of preserved *Convoluta* contains 28,000 specimens. As the individuals are as closely aggregated in a colonial patch as in a tube, we may gain a rough estimate of the numbers in a given area. Allowing, then, that this number (28,000) occurs on a patch of 10 c.c. in area, then 1 square metre would contain 28×10^6 animals. Since we have observed colonies (one of which is drawn on Pl. 30, fig. 1) distributed almost evenly over an area of 200 square metres, their population would not be less than 56^8 .

The *Convoluta* zone of the Trégastel shore is a belt of sand which occupies a definite position with regard to the outflow of sea water due to natural drainage.

On this shore, which presents the ordinary succession from sea to land of muddy sand, fine sand, small gravel, coarse gravel, and pebbles, there is a line more or less broken which marks the outflow of what we may call the salt-water springs. The mode of origin of the line of springs is as follows:—The water brought by the high tide penetrates through the pebbles, gravel, and sand to a certain depth, the depth being determined by the amount of water previously present and the vertical extent of permeable material. As the tide ebbs, this subterranean water, as well as the surface water, recedes, the rate of flow of the drainage water seawards being determined by the obstructions to its course. The outflow of this tidal drainage on the surface of the sand commences at the line of junction of the permeable with the impermeable layers.

Since *Convoluta* is, in all probability, descended from a wholly aquatic ancestor, we must regard its present stations as indicating a progress landwards. Its special equipment of green cells, its high light and heat attunements, its inability to expose itself to light when shaken, all indicate that it can only function as a surface animal,—that is, *Convoluta* is not a sub-aërial, nor is it a marine creature, but is one whose habitat is in a thin film of water; indeed, we find that the characteristic position of the *Convoluta* zone marks the limit of the animal's power to spread landwards. At the upper edge of this zone there is at most tides a constant slow stream of water. Beyond it, landward, the sand becomes dry during low water. Now although *Convoluta*, like lichens, can withstand a very considerable amount of desiccation, yet its habit of swimming down stream in a slow current will prevent it making any considerable headway against stream even though its positive phototropism may start it in that direction. Although, by reason of its positive phototropism, it should succeed in climbing further up the beach, its chances of establishing itself there are very small. For either it will succumb to the combined effects of desiccation and of high temperature, or during some subsequent ebbing tide it will be caught whilst in its lethargic condition and swept back again seaward by the drainage stream, which flows quickly down this steeply sloping part of the beach. In any case, animals extending landwards would be at neap tides, beyond the tide-way, high and dry. Still, it is well to bear in mind that a slight modification of its tropisms might convert *Convoluta* into a thorough land animal. We cannot tell whether, in watching its present distribution, we are watching a creature in course of adaptation to a land habit, or whether it has already reached the limit of its powers in this respect.

The lower limit of the *Convoluta* zone is not so clearly defined, and for good reasons. Local variation in the rate of flow of water from the salt springs will carry patches of a colony seaward. The place where these come to rest will be determined by several factors. Seaward, the slope of the

beach decreases, the rate of flow of the drainage falls off. A point is reached at which *Convoluta* is able to make headway against the slower flow, or by cohering in masses to divert it, and hence to form a new patch. Thus a seaward bound will be set to the *Convoluta* zone, and animals carried further seaward will be destroyed, or returned by the rush of the incoming waters to their former place. That these essays in distribution, now landward, now seaward, are continually going on, may be readily appreciated. A heel-mark in the neighbourhood of the patches forms a little lake into which the drainage water flows, and which soon becomes filled with the dark green scum of *Convoluta*.

2. The Factors that regulate the Formation and Position of the Colonies.

The influence of light in determining the distribution of *Convoluta* is indirect rather than direct. Previous writers, Haberlandt (1891) in particular, have supposed that the phototropism of *Convoluta* is of direct value in enabling this animal to place itself in the area of brightest illumination.

The manifestations of phototropism are so striking in the laboratory that one is tempted to ascribe too high an importance to it. In the laboratory, unilateral illumination of a vessel containing *Convoluta* causes a rapid congregation of the animals about the brighter side. Yet in the open a patch of *Convoluta* may lie tranquilly in a shadow whilst, round about, the ground is bright with sunlight. The explanation of this seems to us to be that the state of tone, compounded of autonomous and light-induced tone, closely determines phototropism. In the laboratory, the tone of the animal is interfered with, and phototropic response, suffering no inhibition, manifests itself with the "certainty of a reflex action;" but in the natural state the reflex action is not certain, a stimulus has to lodge its appeal before the tribunal of tone, and its petition may or may not be granted. Whether a light-stimulus will produce a tropism or not will depend not only on the nature of that stimulus, but also on the

condition of the animal, which condition has been induced among other things by all the antecedent light-stimuli acting not only on the reflex mechanism, but upon the whole nervous mechanism.

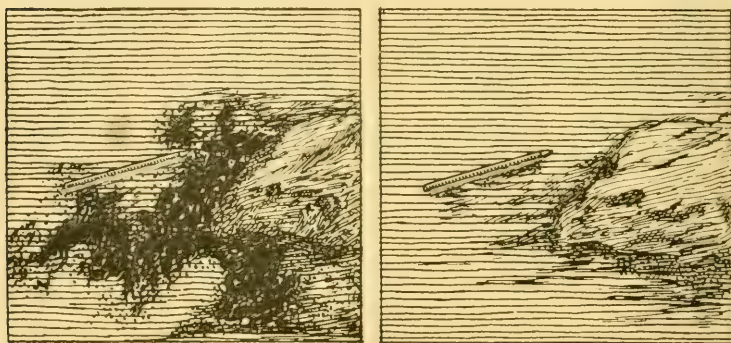
Nevertheless, in the broad way nature uses, the influence of light makes itself felt. This is evident when we consider that the *Convoluta* zone is the most favoured zone with respect to light consistent with a continuous flow of water; so that if *Convoluta* were sown broadcast over the beach, those that escaped destruction would inevitably find themselves brought by the moving waters to this zone. We must therefore conclude that the tropisms of *Convoluta* are all co-ordinated; and that just as the mark of a single reflex is its purposefulness, so is purposefulness the character of the co-ordinated tropisms.

We may sum up the matter thus :—Geotropism in relation to stillness or vibration provides for the vertical distribution of *Convoluta*, bringing it to the surface when the water is withdrawn, and hurrying it from the surface when the waters flow. The need for a film of water and for not too strong a flow, together with the inertia which a dutiful obedience to its many tropisms involves, and the power of sticking closely to its fellows, all make for the gregarious and localised habit that *Convoluta roscoffensis* adopts. Rapid streams of water, produced by local changes in the physical condition of the beach, mark out the barren portions of the zone, and may play havoc with the colony. Thus the distribution, like many distributions, is casual, and the “instinct” of the animal is in favour of parochialism. The young, though capable of swimming freely, remain with the parent colonies, possibly because of the rapidity with which, as we have seen (p. 404), they acquire these tropisms, and also because of their greater power of adhesion to a solid surface in response to the shock of a sudden current of water.¹

¹ Mitsukuri (1901) discusses the influence of light and water on the distribution of *Littorina*, a case with some analogy to *Convoluta*.

3. Variations in the Constituent Patches of a Colony.

As we have already stated, the colonies and their component patches remain in their broad outlines constant day by day. One colony figured on Pl. 30, figs. 1, 2, and under observation throughout July and August, 1902, presented the same outline on the last day as on the first. Nevertheless variations occur. Sudden changes follow the application of a sudden disturbance. Daily and lunar periodic

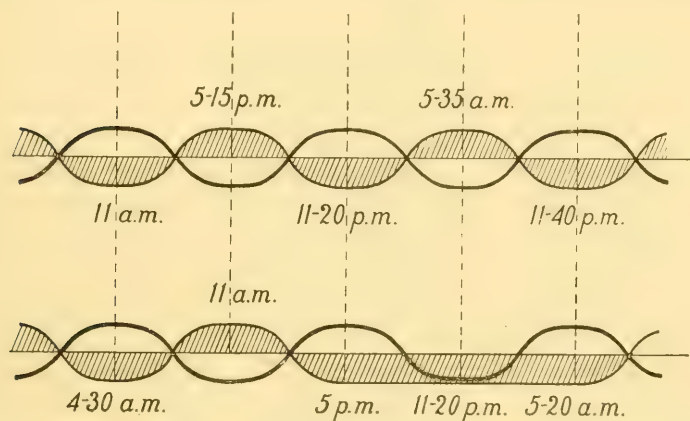


TEXT-FIG. 3.—The two sketches show the influence of vibration on a patch of *Convoluta*. The left-hand figure shows the patch at rest; the right-hand figure the result of tapping gently, and is taken five minutes after the former. The pencil gives the scale. (From photographs.)

changes are also noticeable. Of these we now give some account.

Von Graff (1891) had noticed that by tapping the sand in the neighbourhood of a patch the disappearance of *Convoluta* into the sand could be almost instantaneously effected. Text-fig. 3 is from a photograph illustrating this phenomenon. The interval between the two figures was in this case five minutes; but much shorter intervals, a minute or less, suffice. The depth to which *Convoluta* descends is difficult to determine, but we may say it is such

as to take the animal out of the reach of the disturbing influence. For example, when the tide comes in roughly, the patches disappear before the surface water has reached them. When the tide flows with the gentle quietness of a still summer's day, it may surprise *Convoluta* at the surface of the sand, where they may remain till a ripple gives them the signal to disappear. As the waters withdraw, *Convoluta* begins to rise, and the patches may be re-defined when the water's edge is but a few yards away.



TEXT-FIG. 4.—The two sketches show the daily variation in the amount of *Convoluta* exposed or correlated below the surface of the sand according as to whether the high water is at about noon and midnight (top figure), or is at about 5 a.m. and 5 p.m. The tidal curve is coloured red, and the shading indicates the amount of *Convoluta* above or below the sand, and its rise and fall in relation to the rise and fall of tide.

The reaction, in short, is automatic; and the *Convoluta* are just, and only just, beyond the region of agitation.

Diurnal Variation (Text-fig. 4).—The colonies of *Convoluta* appear at low tide during the day; at night, on the other hand, they do not rise to the surface. During moonlight nights a small patch may here and there be seen.

If a patch be observed at intervals throughout the day, it is found to undergo a sequence of changes in size. On the following day the variation is found to be repeated. As the

tide falls, the patches of *Convoluta* make their appearance and rapidly increase to a maximum size, which maintains itself for several hours and then falls off steadily till the tide turns; and so on day by day. From this it will be clear that each *Convoluta* submits itself to a certain spell of insolation, after which it withdraws from the surface, leaving others, which meanwhile have been shaded by it, to take its place and retire in turn.

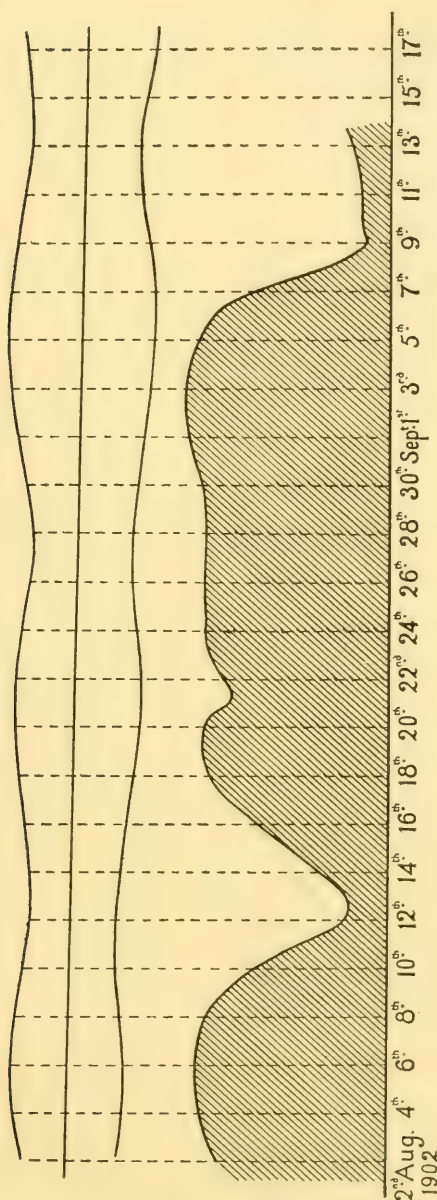
The tidal periodicity which we have recorded in our experiments (Sect. IV, 3, p. 401) manifests itself as a practice steadily recurring in nature.

Lunar Period Variation.—The size of the component patches of a colony undergo a variation, which has a relation to the alternation of spring and neap tides. The text-fig. 5 shows the nature of this variation. As the neap tides give rise to the spring tides, the patches increase to a maximum, only to fall off again during the ensuing week. The extremes of this variation are shown on Pl. 30, figs. 1, 2, and its course for August and September, 1902, are shown on the accompanying text-figure.

The explanation of this variation is probably to be sought in phenomena of reproduction and of growth. The older individuals of a colony are almost invariably in the same phase of growth. Those of a fertile colony become mature simultaneously, and lay their eggs about the same time. This time coincides with the onset of the spring tides. During the antecedent neap tides the animals about to engage in oviposition apparently remain below the surface, where, indeed, the eggs are laid.

4. General Phenomena of Reproduction and Development.

During the summer, certain patches of *Convoluta* remain for months in an immature condition, whereas neighbouring patches pass through a series of mature, alternating with immature, phases. Large numbers of members of these



TEXT-FIG. 5.—The upper figure shows the alternation of spring and neap tides at Trégastel, Côtes du Nord, during August and September, 1902, and is compiled from the local tide-table. The expansions correspond to the springs, the contractions to the neaps. The lower figure shows diagrammatically the variation in the size of the colony of *Convoluta* recorded in the text, and it will be seen that there is a monthly rhythm. The absence of any considerable falling off for the neap tides at the end of August is accounted for by the fact that these tides fell off very little as compared with the previous and succeeding neap tides. Other colonies than the one recorded here showed a distinct fortnightly variation.

fertile patches arrive at maturity simultaneously, and consequently the egg-capsules occur in great numbers at the approach of the highest spring tides. These egg-capsules may be collected on the beach by first tapping the sand and driving the *Convoluta* below the surface, scooping up a little sand, shaking it with water in a test-tube, and catching the slowly sinking white capsules with a pipette.

The general features of the development of *Convoluta* have been described by Georgevitch, but the remarkable phenomena that accompany oviposition have not been previously recorded. The eggs are, or at least may be, fertilised, and the egg-membrane formed within the body of the parent. The discharge of these eggs takes place in one of two ways. In the less general method the eggs are laid singly, and no rupture of the parent takes place. The more general method consists in the discharge of a number (5 to 13), and the formation around them of a mucilaginous capsule. This capsule appears to be secreted by the skin of the parent. In its formation, the body of the animal often undergoes violent changes. Rupture of the tissues, and indeed a complete break across the middle of the animal, usually follow. The spent anterior end crawls away, responsive, like the intact animal, to the directive stimuli of light and gravity. The tail end, devoid of tropisms, ejects the spermatozoa, remains for a time attached to, or in the neighbourhood of, the egg-capsule. It may swim ceaselessly in devious spirals, then come to rest, and after a day or two disintegrate.

The surface of the capsule is sticky at the time of laying, and adheres to sand particles, thus being anchored. It is covered more or less closely with the disjecta of the parent, which afford a nidus for the development of many other organisms (Pl. 30, fig. 3). The eggs are laid as well in darkness as in light. The embryos usually hatch in from five to seven days, though the incubation period is very variable. Before hatching, the embryos may be seen revolving vigorously within the membranes, and occasionally, owing to exceptional thickness of the membrane, the rotating stage is

prolonged. During this phase the animal is flexed ventrally, both longitudinally and transversely. The otocyst is present, the wall being lined with fatty globules. The whole body is full of similar fatty granules of varying size, which granules stream inwards and outwards in obedience to muscular contraction. The epidermal orange-red glands are already present. The eyes, however, are indistinguishable. Very characteristic of the revolving phase is the presence near the hinder end of the body of a large coloured vacuole, brown or yellowish. It lies ventrally in a nucleated meshwork, the foundation of the inner parenchyma or gut. Within the vacuole one or more refractive fatty globules and spicules of unknown significance are frequently found. This vacuolated structure undergoes marked variations of shape; at one time it is spherical, at another irregularly branched. During microscopical examination it frequently collapses, and its contents immediately disappear. This coloured vacuole is found, though less sharply defined, in just hatched *Convoluta*, disappearing after the first day or two.

When the young *Convoluta* is ready to hatch out, the egg-membrane splits equatorially (Pl. 30, fig. 3 B). The society of larvæ, after creeping and swimming within the capsule, suddenly leave it, passing with ease through the thin walls, to which they frequently return after a short spell of activity. As we have pointed out in Sect. II, there are good grounds for believing that the food of *Convoluta* is supplied by the varied organisms living on and in the egg-capsule. For days, however, isolated larvæ will live in sterilised water, developing at the expense of the fat with which their tissues are supplied. As this fat is gradually absorbed from the "inner parenchyma" or gut, this tissue contrasts more strongly than before with the still fat-laden peripheral parenchyma (Pl. 31, fig. 15). Ultimately, if no food is supplied, the *Convoluta* becomes more and more vacuolated, exhibiting phenomena of starvation very similar to those described by Wallengren (1902) in *Paramecium*.

The disappearance of fat from the otocyst, and the develop-

ment of the eyes, take place during the first two or three days, and afford a useful mark by which such larvæ may be readily distinguished from just hatched *Convoluta*. Under natural conditions the food of young *Convoluta* consists of algæ, diatoms, and other organisms, as described on p. 370. The evidence that from such a mixed infection *Convoluta* produces a pure culture of "green cells," digesting the remainder, is given in Sect. III.

Section VI.—SUMMARY.

1. Food.

A. Previous Observations.—Previous observers have failed to demonstrate the presence of ingested solid food in either the larval or adult stage of *Convoluta*. Geddes, von Graff, and Haberlandt concluded that *Convoluta* does not feed, but that the animal derives its food-material from the products of the photosynthesis carried on by its green cells.

Geddes and Haberlandt were confirmed in this conclusion on finding that the animal, when placed in darkness, dies in the course of two or three days.

B. Observations by the Authors.—Our observations stand in direct contradiction to these. *Convoluta* feeds, and feeds voraciously. From the time of hatching up till the time of commencing maturity, *Convoluta* (1 to 5 mm. long) ingests diatoms, algæ, spores, grains of sand, and colonies of bacteria. It also takes up such substances as litmus, congo-red, etc., with avidity. Mature and immature specimens digest masses of their own green cells, the discoloured remains of which form conspicuous brown clumps in the gut.

Moreover we have maintained *Convoluta* alive in complete darkness for more than a fortnight, and find that the starch of the green cells disappears with extreme slowness—not till after five days of darkness in young (1 to 2 mm. long) animals; seven days in adults.

We conclude—

(1) That *Convoluta* has not lost its power of independent nutrition.

(2) That the animal obtains little if any food by the translocation of the reserves of its green cells.

(3) That the sand in which *Convoluta* lives is not barren of other life, as von Graff supposed, but that it supports a rich and varied flora and fauna.

We have demonstrated the dependence of starch-formation in the green cells on the presence of light, by maintaining animals in darkness till all reserve starch has disappeared and then exposing them to light. Starch makes its appearance in the green cells after less than ten minutes' exposure to bright sunlight.

By the use of monochromatic screens, we show that the rays which are most active are—as in plant chloroplasts—those between B and C (Fraunhofer lines); that no assimilation (as measured by reserve starch) takes place in the green; that some occurs in the blue. The spectrum of the alcoholic extract of chlorophyll of *Convoluta*, examined by the hand-spectroscope, shows the chief absorption band of chlorophyll (between B and C) and strong absorption of the blue end.

2. Development of the Green Cells.

A. General.—Direct proof that the green or yellow cells of Protozoa, Cœlenterates, Turbellaria, and other animals are due to an infection from without has been obtained only in the cases of sea-anemones (Brandt), *Hydra viridis*, and *Stentor* (Beyerinck and Famintzin). The pure cultures, in the latter cases, have been identified with the green alga, *Chlorella vulgaris*. A similar origin by infection is assumed for the green cells of other animals, and the relation is generally regarded in all cases as a symbiosis.

B. Previous Observations.—With respect to *Convoluta*, Haberlandt failed to cultivate the green cells.

Observing their remarkable histological features (absence of cellulose wall, etc.), he put forward the hypothesis that the green cells are now parts of the animal—animal cells to which a leucoplast is transmitted from the egg.

Georgevitch hatched out *Convoluta*, showed that it develops as a colourless larva, and claims that such a colourless larva, if kept in sterilised water, fails to develop green cells, and dies within two days. He concluded that the green cells gain access to the animal from the sea water.

c. Experiments of the Authors.—Our experiments lead us to the following conclusions :

(a) A leucoplast cannot be detected in the egg.

(b) *Convoluta* hatched in sterilised water may live for two weeks therein.

(c) The first indication of the future green cell is colourless, and not green. Infection, if it occur, is by a colourless cell.

(d) The precautions to ensure sterile conditions, taken by Georgevitch and by ourselves in our earlier experiments, are useless. In these experiments the egg-capsule was placed in sterilised water; we find, however, that the egg-capsule bears a rich and varied collection of green, pale green, and colourless cell colonies.

(e) Contrary to Georgevitch's statement, when hatched from egg-capsules placed in sterilised water, *Convolutas* are found in a certain number of cases to develop green cells. Hence either the green cells are not the result of infection, or infection may take place from the capsular flora.

(f) The latter alternative is probably correct, for the more precautions are taken to protect larval *Convoluta* from infection, the fewer are the cases in which green cells or their colourless antecedents make their appearance in the animals.

(g) The colourless antecedents of the green cells are first seen in the gut, just above the mouth.

d. Conclusions.—Direct proof of infection is lacking.

The evidence, however, points most strongly to infection. The infecting organism is a colourless cell. Infection often takes place from the capsule. The situation and colourlessness of the infecting cell suggest the view that this cell is a saprophytic stage in the life-history of the green cell. Such saprophytic colourless stages are well known in green algæ, diatoms, and Flagellates.

The colourless cells are taken up in company with other organisms. A pure culture is made from this mixed infection in the gut of the animal. There the cells become green, divide, and, continued in wandering cells, are carried to their final station in the periphery of the body.

We regard the presence of the green cells as due to a peculiar and special case of phagocytosis in which neither green cell nor wandering cell is destroyed.

The relation between animal and green cell is a complex one, and cannot be described as symbiotic. The green cell once in the body of the animal probably never escapes; either it is digested or it dies when the animal dies (p. 375).

3. Tropisms.

A. Previous Observations.—Geddes (1879) first recorded positive phototropism (phototactism). Von Graff and Haberlandt (1891) observed negative geotropism in stillness, positive geotropism in the presence of vibrations.

B. Observations of the Authors.—(a) Geotropism.—The observations cited above were confirmed. The young at hatching react to gravity in the same way as adults. In the absence of the otolith, geotropism does not occur.

The reflex mechanism involves the anterior end of the body. The hinder end of animals divided transversely does not react to gravity.

(b) Thermotropism.—*Convoluta* is attuned to a high light-intensity. It is athermotropic at ordinary temperatures. Just below the lethal point (38° C.) it is negatively thermotropic. The response, however, is singularly and often fatally imperfect.

(c) Phototropism.—*Convoluta* is positively phototropic, but only under certain conditions. A sudden elevation of light-intensity induces a negative phototropism. Background may inhibit phototropic response.

At the moment of hatching, *Convoluta* is aphototropic. The power of response to light develops rapidly, appearing a few hours after hatching.

The anterior end only, of animals divided transversely, is phototropic.

The rays active in producing phototropism are the green. The blue rays, which are active in inducing movement in zoospores, in *Euglena*, and in plants generally, produce no tropic effect in *Convoluta*. The red rays produce a feeble negative tropism.

The tonic influence of light is more important than the tropic influence. To the former influence is due the remarkable periodic "tidal" movement which, as we have found, *Convoluta* performs. After a spell of insolation, colonies sink below the surface, and after a certain sojourn in darkness they return to the surface. These movements synchronise with the covering and uncovering of the *Convoluta* zone by the tides. They take place in colonies brought into the laboratory, but do not occur when such colonies are kept in darkness. *Convoluta*, after a certain spell of illumination, passes into a condition of light-rigor. In this condition it is singularly inert and susceptible to mechanical injury.

(d) Rheotropism.—*Convoluta* reacts to changes in rate of flow of water. In a moderate stream it tends to move up stream. Under the stimulus of a suddenly increased flow it sticks to the ground; when this is impossible it contracts itself and is carried down stream.

4. Ecology.

A. Previous Observations.—Geddes and von Graff have recorded the distribution of *Convoluta* along the shores of the Île de Batz, Roscoff. They describe the rapid

disappearance of the colonies when the sand is tapped or when the tide flows over them. They suggest that light and gravity provide the stimuli whereby these movements are regulated.

B. Observations of the Authors.—The *Convoluta* zone is determined by the outflow of drainage tidal water. The upper limit of the zone corresponds to the high-water mark of lowest neap tides. This situation ensures the maximum of light-exposure consistent with security from desiccation. *Convoluta* is neither a sub-aërial nor a marine animal. It lives in a film of water, and has migrated from the sea shorewards to the highest level consistent with aquatic life. The stations occupied by *Convoluta* are remarkably constant. The constituent patches of a colony may be recognised day after day for months together.

Nevertheless diurnal and fortnightly variations in the size of the colonies occur.

The diurnal variations are tidal; each patch reaches its maximum size soon after its site is exposed. The size slowly decreases till the tide comes in. When the tide comes within a few feet, the patch disappears suddenly. At night, the colonies do not ascend.

In addition to its daily variations, *Convoluta* exhibits a fortnightly lunar variation. The colonies, with their constituent patches, increase to a maximum during spring tides, decrease to a minimum during neap tides.

The daily variations are due to the tonic effect of light; in which tonic effect must be included the "after-effect" of prolonged light-exposure.

The fortnightly variations are due to periodicity of reproduction. The majority of animals of a mature colony discharge their eggs in egg-capsules at the onset of the spring tides. The capsules are laid beneath the sand. In most cases the body of the animal is ruptured during the process of laying. The hinder half remains in the sand, the head end rises and joins the patch. Thus at neap tide the size of the patches, and hence of the colony, is decreased.

The colonial habit of *Convoluta*, which distinguishes it from its allies, appears to be an indirect result of its tropisms. In obedience to tropic stimuli, it becomes adept at vertical movements, to the exclusion in very large measure of horizontal movements.

The lethargic state induced by prolonged light and prolonged darkness also tends to preserve groups of *Convoluta* on the patch to which they belong. Gregariousness is, in this view, a negative quality.

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EXPLANATION OF PLATES 30 & 31,

Illustrating Messrs. Gamble and Keeble's paper on "The Bionomics of *Convoluta roscoffensis*, with especial Reference to the Green Cells."

PLATE 30.

FIGS. 1 and 2 represent the appearances of a colony formed by *Convoluta roscoffensis* on a beach at Trégastel, Côtes du Nord. Fig. 1 is the average appearance at low-water spring tides; Fig. 2 the extent of the same colony at low-water neap tides. The figures show that the colony is formed of green patches (each of which is remarkably constant), and that the patches occur high up on the shore and are related to the outflow of the salt springs (shown in streaks and described on p. 408). It will be seen that the patches are far more extensive at spring tides than at neap tides. The explanation of this phenomenon is given on p. 414. A diagram of this lunar variation is given on p. 414. The horizontal scale of the figures is $\frac{1}{2\frac{1}{10}}$ of the actual. This colony was kept under daily observation from July to September, 1902. The position and extent of the constituent patches at the beginning and end of this two months' record were precisely the same.

FIG. 3.—This figure represents the egg-capsule of *Convoluta roscoffensis* and the organisms which infect it. *A* is the capsule with its eggs. *B*. A capsule with the embryos just hatching out. *C*. Linear masses of a colourless refractive spore-like organism. They possess a definite wall, which, however, gives no cellulose reaction with Schütze's fluid. The contents exhibit active movement. The average diameter of these spherical granules is 5μ , the smallest 2.5μ . *D*. Spherical colourless cells $15-45\mu$ in diameter, the contents of which are granular, spongy, or heart-shaped in surface view. These cells have no definite wall. *E*. Active ciliated organisms $20-30\mu$ long, and filled with refractive, often green globules. *F*. Pale green cell-colonies 25μ in diameter. *G*. Spores with a thick wall containing a finely granular plasma and a mass of refractive globules. When extruded the globules swim actively by one or two flagella. *H*. Brown algæ of a dumb-bell shape and provided with several distinct peripheral chloroplasts. *K*. Diatoms. *L-Q*. Part of a filamentous algal thallus found by the authors on one occasion attached to a *Convoluta* egg-capsule. It possesses peculiar clear terminal cells, and bifurcated structures at the apex of empty cells. The object of introducing these figures is to emphasise the difficulty of obtaining larval *Convoluta* free from infecting organisms. Many of these structures (*G*, *H*, *K*, *C*) are to be found in the body of the parent at the time

of laying the egg-capsule, and it is therefore as possible that these organisms are the result of disintegration of the hinder end of the parent as that they have subsequently migrated from the water to the capsule.

FIG. 4.—*Convoluta roscoffensis* (0.2 mm. long) one day old. The specimen was one of a batch hatched in an egg-capsule laid in a dish with other *Convoluta*. It has already ingested a grain of sand, a mass of brown algal cells (*X*), a blue-green alga (*Y*), and contains in addition a fully formed "green cell" (*G. C.*) and developing green cells (*A* and *B*), three of which form a group obviously arising by subdivision of a single colourless cell. Within these three cells, indications of the future chloroplasts are visible as peripheral globules. The grain of sand is enclosed by the wandering cell (*PHAG.*).

FIG. 5.—*Convoluta roscoffensis* one day old. It was placed at the moment of hatching (in sea water with the capsule) into a jar with congo red suspended in the sea water. The figure shows that this *Convoluta* has ingested two algal cells (*AL.*) as well as masses of congo red. The acidity of the vacuoles round the latter is shown by the edges of the congo red having taken on a blue colour.

FIG. 6.—A similar specimen similarly treated with methylene blue. The colouring matter is taken up by the wandering cells (*M. BL.*), and has formed a diffuse coloration in the region of the gut.

FIG. 6A.—The figures A, B, C, D, represent stages in the degeneration of developing green cells within the bodies of young *Convoluta* bred in darkness and fed with litmus, and illustrate a number of experiments. Just hatched *Convoluta* were placed in darkness on August 24th, 1902, and were drawn on September 4th. Older specimens which had developed a few "green cells" in daylight gave a similar result. The figures show that starting with a typical green cell (*A.*), continued darkness and starvation induce the breaking up of the chloroplast, the gradual loss of colouring matters, and ultimately the formation of a mere heap of fat globules. Fat globules, also the remains of degenerate "green cells," are seen in Pl. 31, fig. 18. Cf. the text, Section III, p. 393.

PLATE 31.

FIG. 7.—An immature but full-grown *Convoluta roscoffensis*, to show the masses of dark brown granules (*X*₁, *X*₂, *X*₃), which occur regularly in specimens examined immediately after capture. The figure gives a good idea of the appearance of the individuals of sterile patches; but the brown masses are found in mature as well as in immature specimens. There is good reason for believing that these brown masses are the discoloured remains of *Convoluta*'s "green cells" digested by the gut. The otocyst, eyes, and mouth are also indicated.

FIG. 8.—A very young *Convoluta* (0.157 mm. in length when contracted), to show the development of the "green cells." The specimen was hatched in sea water, August 21st, 1902, and placed in the open from that day till August 23rd. It was then drawn. The eyes (*OC.*) had developed, and colourless, yellow, and green cells were present. The figure shows the distinct leucoplasts, the pyrenoid, the gradual development of chlorophyll and of the stigma. On testing for starch a colourless and yellow cell gave a distinct reaction (*A. B.*).

FIG. 9.—A specimen (0.35 mm. long, somewhat contracted) taken on the shore at Trégastel, September 5th, 1902, and drawn to show the numerous diatom frustules (*Diat.* and *R.*) with which its gut was filled. The figure is typical of many *Convoluta* 3—4 mm. long. It shows that the previous view maintained by Haberlandt and Georgevitch of the abstinence of *Convoluta* from solid food is incorrect.

FIGS. 10 AND 11.—Remains of diatoms from a specimen of *Convoluta* 4.86 mm. long, full-grown but immature. In Fig. 10 the remains are hardly recognisable.

FIG. 12.—A specimen 0.42 mm. long, hatched in sea water, and drawn a few hours after hatching. The fat is still present in the ootocyst. The eyes have developed exceptionally rapidly. Fat is still abundant in the peripheral parenchyma. In the gut a large phagocyte (*PHAG.*) contains several developing "green cells" in the colourless early stage. These colourless cells vary in the size and nature of their contents. The largest cell is 0.012 mm. in greatest width, the smallest is 0.006 mm. The contents are either mere globules of fat or curved and yellowish leucoplasts in which chlorophyll is just developing. The glands (*GL.*) are indicated.

FIG. 13.—A specimen hatched in sea water and drawn the following day (September 12th, 1902). A group of five developing "green cells" are shown with the chloroplasts already established.

FIG. 14.—A specimen hatched in sterilised water and drawn a few hours afterwards. Two developing green cells are shown. One (*C. G. C.*), enclosed in a multinucleate phagocyte (*PHAG.*), contains several peripheral leucoplasts; the other, also enclosed in a wandering cell, shows the excentric nucleus but no distinct leucoplast.

FIG. 15.—A specimen of *Convoluta roscoffensis* a week after hatching in sea water. Only three green cells are present (*G. C.*). The figure shows the mouth (*Mo.*), the nucleated phagocyte that guards it (*PHAG.*), the central parenchyma or gut now free from fat, the peripheral parenchyma in which fat is still abundant streaming inwards and outwards as the musculature constrains it.

FIG. 16.—This specimen hatched from a capsule placed in water sterilised at 60° C., and placed in darkness on August 18th, 1902. On August 28th the *Convoluta*, being then presumably about three days old, was put in the

open, and was drawn on August 29th. The weather on August 28th and 29th was dull. The sketch shows a mass of developing green cells, still, however, all colourless, in the phagocyte (*PHAG.*) that guards the mouth; two colourless cells near the hinder end (*C. G. C.*); and a group of three more advanced cells (*C. G. C.*) evidently arising by division.

FIG. 17.—A specimen hatched from the same stock as Fig. 16, in darkness and sterilised water. It was drawn on August 30th, after exposure to daylight for a few hours, during which time but little direct sunlight was available. It measured 0.39 mm. in length, and exhibited colourless predecessors of green cells (*C. G. C.*), remarkable nucleated structures (*X*) of unknown significance, and one "pulsellum" (*Puls.*), the nature of which is still unknown in spite of the work of Geddes, Delage, and ourselves.

FIG. 18.—A specimen from the same stock, and hatched under the same conditions as the two previous ones, but maintained in darkness till September 3rd. It now measured 0.5 mm. in length, but the only trace of its colourless cells is to be seen in the aggregated fat (*G. C. degen.*). The effect of starvation is seen in the vacuolation of the gut (*Vac.*). Several developing pulsellæ (*Puls.*) are present. The degeneration of developing green cells to mere heaps of fat is also seen on Pl. 30, fig. 6A.

FIG. 19.—A specimen .45 mm. long, hatched with parents in sea water in the light of the laboratory. The figure shows many interesting points in the development of the green cells. Three distinct forms occur: the ordinary green cells (*G. C.*), the colourless cells (*C. G. C.*), and small yellowish bodies (*S. G. C.*), which, as the side figures *B* and *C* suggest, are probably budded off from the green cells. The tract of modified protoplasm that forms a phagocyte is here specially large, and within it several colourless and small yellow cells occur. The retention of the colourless phase of the green cells is an interesting feature. *A*, *B*, and *C* show other features in the structure of the green cell (chloroplast and stigma, *St.*).

FIG. 20.—A young *Convoluta* 0.745 mm. long, from the beach, which shows the retention of the colourless cells (*C. G. C.*) and the gradual development even at this comparatively late stage of the life-history of the chloroplasts. At the hinder end of the animal this process is evidently at work. The stigmata (*St.*) were particularly clear in the young green cells of this specimen.

FIG. 21.—Two colourless cells from a specimen 0.35 mm. long, hatched in sea water September 10th, and drawn September 19th, 1902. The figures show the variable form and extent of the leucoplast (*Chl.*), the nucleus, and the refractive granules.

Trypanosoma in Birds in India.

By

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Liverpool.

With Plate 32.

THE comparatively recent discovery of the presence of trypanosoma in man as a cause of disease by Dutton, Castellani, and others has opened up a field of interesting research. In view of the help which has been afforded in the investigation of the malaria parasite in man by the study of similar protozoan infections in animals, chiefly birds, it might be of service to record the presence of trypanosoma parasites in the blood of birds in India. The life history of these Protozoa will very probably be first elucidated and worked out in the lower animals. From the cases recorded by Dutton and Manson, and the possible relationship of these parasites to sleeping sickness, they have now become more than pathological curiosities.

In India, in 1900, whilst examining the blood of the domestic pigeon affected with *Halteridium Danilewskyi*, I came across a species of trypanosoma in these birds which I now describe. The parasites were comparatively few in number in the blood, and the percentage of birds affected was not a large one. Their presence in the blood did not appear to affect the health of the birds in any way.

From the accompanying illustration of the pigeon parasite

(fig. 1) it will be seen that the organism is of large size, showing a total length of 45 to 60 μ , and a breadth of 6 to 8 μ . Stained by the Romanowsky method, it is seen to possess a large centrally placed macronucleus extending the whole depth of the parasite, and much deeper than long; the micronucleus or centrosome is very small, and stains very deeply; close to the centrosome is a clear spot or vacuole.

The protoplasm is not uniform in staining, but shows here and there lighter coloured patches, and in some forms distinct evidence of longitudinal striation of the protoplasm is observable. Scattered through its substance, especially towards each end, are granules of a dark violet colour. The anterior end of the body is much elongated, pointed, and gradually merges into the flagellum, so that it is difficult to say where the body ends and the free portion of the flagellum begins. The flagellum originates from the micronucleus, and proceeding forwards along the outer side of the undulating membrane to the anterior end, it becomes free. This free portion of the flagellum is exceedingly fine and attenuated.

At the posterior end the body also tapers, and ends in a pointed extremity, which stains a little less deeply than the other parts of the protoplasm; it has dark violet granules.

The undulating membrane is very distinct but narrow; it can be seen proceeding from the neighbourhood of the micronucleus forwards to the anterior end of the body.

Major Ross has kindly allowed me to examine some slides of the blood of crows made by him in 1898 in India. These contain trypanosomata, but of an apparently different species from that already described; their length, however, appears to be about the same.

These specimens from the crow (fig. 2) were faintly stained with methylene blue, and owing to the length of time since mounting they had somewhat lost their colour. I am therefore unable to describe them as minutely as I should have liked, chiefly as regards the position and size of the macronucleus.

The chief points in the trypanosoma from the Indian crow

are the rather abrupt termination of the posterior extremity ; the breadth of the parasite ($3-4.8\mu$) is not so great as that of the parasite in the pigeon, and the micronucleus is also much nearer the posterior end.

The crow trypanosoma has more of the shape of *T. Lewisii* or *T. Brucei* ; it is, however, much larger.

In anticipation of further work being done on these interesting Protozoa, and for purposes of identification, I give the following measurements :

Trypanosoma of domestic pigeon (Indian)—

Length of organism	45—60 μ .
Breadth of organism opposite nucleus	6—8 μ .
Length from micronucleus to posterior end	19—22 μ .
Length from micronucleus to centre of macronucleus	4—6.5 μ .
Length from macronucleus to anterior end	25—30 μ .
Depth of undulating membrane7 μ .

Trypanosoma of crow (Indian)—

Length of organism	40—56 μ .
Breadth of organism	3—4.8 μ .
Length from micronucleus to posterior end	8—9.5 μ .
Length from micronucleus to anterior end	32—46.5 μ .

Amongst the group Mammalia several species of trypanosoma have been described. Gros, in 1845, found a parasite much resembling a trypanosoma in the blood of the field-mouse. Lewis, in 1879, described a species (6) which was found to be exceedingly common in the blood of rats (*Mus rattus*, *decumanus*, and *rufescens*), also in the hamster (*Cricetus arvalis*). The length of this organism, including the flagellum, is $24-25\mu$, and its breadth 1.5μ . In many cases 25—29 per cent. of wild rats are found infected. In India (Bombay) 12 per cent. of the rats harbour the parasite.

Laveran and Mesnil have shown that the disease can be conveyed from rat to rat by the agency of fleas.

Surra, a disease affecting horses and mules in India and Burmah, has been shown by Evans to be due to a trypanosoma (*T. Evansi* [7]).

Lt.-Col. Bruce, in 1896, described the occurrence of nagana amongst horses and cattle in Central Africa, and probably in other parts, and discovered the cause to be a trypanosoma (*T. Brucei* [8]) in the blood of the animals.

In South America a disease, mal de caderas, very similar to surra and nagana, has been described. In this case also a similar parasite has been discovered as the causative agent, which Laveran and Mesnil state to be identical with that of nagana.

Comparing *T. Lewisi* of the rat with *T. Brucei* of nagana, the former is much thinner; it is not so long as *T. Brucei*, which varies from 26 to 28 μ . The posterior end of *T. Lewisi* is pointed; that of *T. Brucei* is blunt. *T. Brucei* has a large centrally placed macronucleus, and the body has many curves.

From the work of Koch (9) in connection with the parasites, and of Rodgers (10) on the symptoms of surra and nagana, it is not improbable that these two diseases are identical, though this has not been proved.

Bloodsucking flies, such as horse-flies (*Tabanus*) and the tsetse fly (*Glossina*), are the transmitting agents in these diseases.

In dourine (11), a disease affecting horses, the trypanosoma parasites (*T. equiperdum*) are rare in the blood, but occur mostly in the sero-sanguineous fluid in the local œdemas, and in the mucous membranes of the parts affected.

In February, 1902, a large and distinct species of trypanosoma pathogenic to cattle was discovered by Dr. Theiler (12) in the Transvaal.

The most interesting development regarding these parasites, however, is the comparatively recent discovery of their presence in the blood of man in Africa by various observers

(13), chiefly Dutton, who definitely recognised and figured these organisms in his report in 1902 (14).

Since then Castellani, working on the Royal Society's Commission on sleeping sickness, has discovered these parasites in the blood and cerebro-spinal fluid of patients suffering from this disease in Uganda, and Bruce has shown that 25 per cent. of the population on the north shore of the Victoria Nyanza have this parasite in the blood.

Species of trypanosoma, as parasites in animals other than Mammalia, have been from time to time described.

The original trypanosoma (*T. sanguinis* [1]) was discovered in the blood of species of frog (*Rana esculenta*, *temporaria*, and *Hyla arborea*) by Gruby in 1843.

T. Eberthi (2) was described in 1861 as occurring in the intestine of birds.

The discovery of *T. Balbiani* (3), in 1882, in the intestinal canal of *Ostrea edulis* and *angulata* showed that these parasites are not confined to the group of the Vertebrata; and Labbé, in 1891, described *T. Danilevskyi* (5), which he found in the intestine of leeches; these, however, had apparently sucked the blood of horses or asses.

Amongst the group of fishes trypanosoma parasites have been described chiefly by Mitrophanon in 1884, in *Cobitis fossilis* (*T. cobitis* [4]), also in *Tinca vulgaris* and *Carassius vulgaris* (*T. carassii* [4]).

As far as I can ascertain from an examination of the literature of the subject, these parasites in the blood of birds have not been hitherto described.

Eberth, in 'Zeitschrift für wissenschaftliche Zoologie,' vol. xi, p. 98, has described a trypanosoma in the intestine of birds; these were found in the Lieberkuhn's glands of the cæcum and ileum, but from his description it appears to be a totally different parasite from that above described.

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On the Modification of the Eye Peduncles in Crabs of the Genus *Cymonomus*.

By

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With Plates 33 and 34.

My attention was drawn to the interesting subject which is dealt with in the present article by a paragraph in Lord Avebury's charming little book, 'The Beauties of Nature.' He there says (p. 331 of the last edition), "Sir Wyville Thomson mentions a kind of crab (*Ethusa granulata*) which, when living near the surface, has well-developed eyes; in deeper water—100 to 400 fathoms—eye-stalks are present, but the animal is apparently blind, the eyes themselves being absent; while in specimens from a depth of 500 to 700 fathoms the eye-stalks themselves have lost their special character, and have become fixed, their terminations being combined into a strong pointed beak." When I came upon this passage it occurred to me that possibly the crab was large enough to form a suitable "exhibit" for the public gallery of the Natural History Museum, and that if so the three stages indicated in Lord Avebury's brief notice would constitute a very interesting and striking demonstration for the general public of the modification of the organ of sight of Crustacea in relation to the presence or absence of light in their environment.

I therefore made inquiries, and found that the specimens dredged by the "Porcupine" in 1869-70, referred to by Lord Avebury, were still in the possession of my old and valued friend the Rev. Canon Norman, F.R.S., who had in 1873 published a description of them. It is a very short one, without figures, and remains the only account we have of these remarkable specimens. Canon Norman at once placed the specimens in my hands (in November, 1902). I found them to be too small for public exhibition. Canon Norman

FIG. 1.

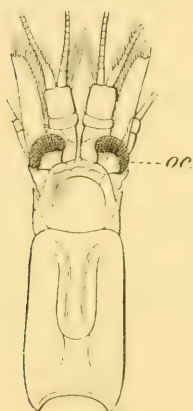


FIG. 2.

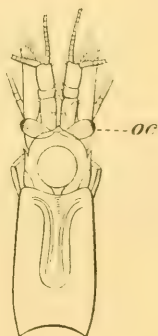


FIG. 1.—*Boreomysis obtusata*, G. O. Sars. 345 to 2740 fathoms. "Eyes normal." Sars, 'Schizopoda,' pl. xxxiii, fig. 2.

FIG. 2.—*Boreomysis microps*, G. O. Sars. Female, $\times 6$. 1250 fathoms. Eyes of smaller size. Sars, 'Schizopoda,' pl. xxxiii, fig. 7.

also gave me the beautiful drawings of the specimens made twenty-five years ago by the late Mr. Albany Hancock, which are now at last published, forming the plates accompanying this article (Pls. 33 and 34). He also furnished me with references to the published notices of the specimens of *Cymonomus* (*Ethusa*), with more or less modified eye-stalks, as well as with references to the literature of the genus; and whilst urging me to undertake the writing of notes to accompany a publication of the drawings—a task which he did not

wish to undertake—he suggested that the account of the facts concerning *Cymonomus* should be illustrated by some figures of the strange modifications shown by the eye-stalks of several deep-sea Mysidæ. These are illustrated in the woodcuts (see text-figures 1 to 7 and accompanying explanations).

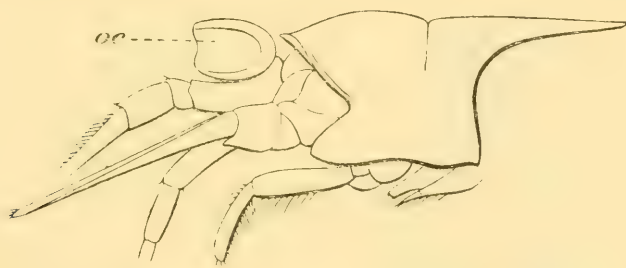


FIG. 3.—*Boreomysis scyphops*, G. O. Sars. Adult female. 1900 fathoms. No ommatidia. The ocular peduncles are converted into cup-like plates. Sars, 'Schizopoda,' pl. xxxii, fig. 4.

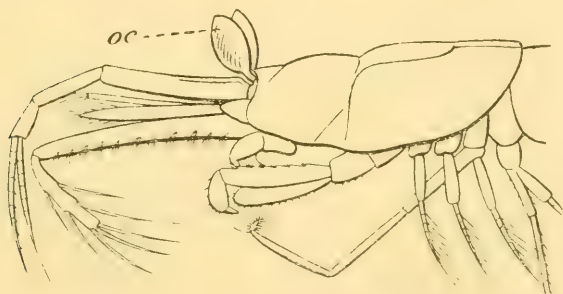


FIG. 4.—*Petalophthalmus armiger*, Willem. Suhm. Male, $\times 4$. 2500 fathoms. No ommatidia. The ocular peduncles are converted into mobile leaflets. Sars, 'Schizopoda,' pl. xxxii, fig. 1.

Apart from these interesting cases in the Schizopoda, the modification of the eyes in deep-sea decapod Crustacea is now recognised as a very frequent occurrence. The degree of degeneration of the optical apparatus and accompanying modification in the character of the ocular peduncles varies from a simple suppression of the ophthalmic pigment and

of the corneal facets (whilst the general form and demarcation of the corneal area is retained) to the complete

FIG. 5.

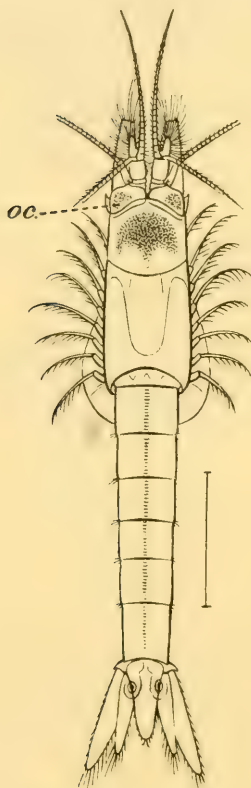


FIG. 6.

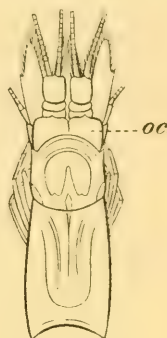


FIG. 7.

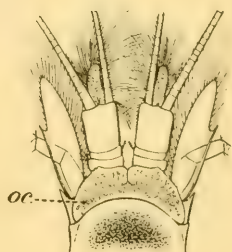


FIG. 5.—*Amblyopsis abbreviata*, G. O. Sars. Norway coast, 100 to 300 fathoms. No ommatidia. The ocular peduncles are seen as two broad plates. 'Carcinologiske Bidrag,' pl. vi, fig. 2 (and 22).

FIG. 6.—*Amblyops Crozetii*, Will. Suhm. Male, $\times 5$ times. 1600 fathoms, S. Pacific. The ocular peduncles are united in front of carapace. Sars, 'Schizopoda,' pl. xxxiii, fig. 11.

FIG. 7.—*Pseudomma roseum*, G. O. Sars. Lofoden Isles, 400 fathoms. No ommatidia. The ocular peduncles form a broad plate with peculiar internal arborescent structure. Sars, 'Carcinologiske Bidrag,' pl. iv, fig. 25.

disappearance of that area as a distinct structure, and the alteration of the shape and character of the eye-stalk. The

following list of such modifications in deep-sea Decapoda is given by Dr. Ortmann in the fifth volume of the new issue of Bronn's 'Thierreich' (1899), parts 53, 54, and 56, p. 1191 :

"*Psalidopus*, in 400—500 fathoms depth, has eyes without pigment and without facets.

"Some species of *Pontophilus* have pale pigment, but in other respects well-developed eyes.

"*Prionocrangon* (200—500 fathoms) has no eyes.

"All *Eryonidæ* are blind: the eyes are reduced to a stump.

"In *Phoberus* the eyes are small and reduced.

"In *Thaumastocheles* they are entirely gone.

"In *Nephropsis* they are reduced.

"*Eiconaxius* has the pigment pale (even in the deeper part of the littoral zone, where it lives in the inside of sponges).

"In *Calastacus* and *Calocaris* the eyes are devoid of pigment and of facets. Among the Paguridea, *Chiroplatea* presents only conical eye-stalks. *Catapaguroides microps*, A. M. E. et Bouv., has degenerate eyes.

"The sub-family *Munidopsinæ* (five genera and many species) is characterised in distinction from the *Galatheinæ* by the reduced eyes.¹

"Among the *Dorippidæ*, *Cymonomus* is blind, and in *Cymonomops* the eye pigment is wanting; in *Ethusina*—in contrast with *Ethusa*—the eye-stalks are not capable of movement, and the eyes are reduced.

"An interesting case is presented by one of the *Brachyura*, *Bathyplox typhlus*, A. M. E., in which, when occurring at depths of 400 to 450 fathoms, very short eye-stalks with undeveloped corneæ are found; whereas, in examples which are taken in shallower water, the short eye-stalk carries a small but distinct cornea."

The foregoing summary, relating to the eyes of Decapoda only, was published in 1899.

The description by Dr. Norman of his *Ethusa granu-*

¹ See Figs. 8 and 9.

lata (subsequently placed in his new genus, *Cymonomus*, by Alphonse Milne-Edwards) was published in 1873 in a British

FIG. 8.

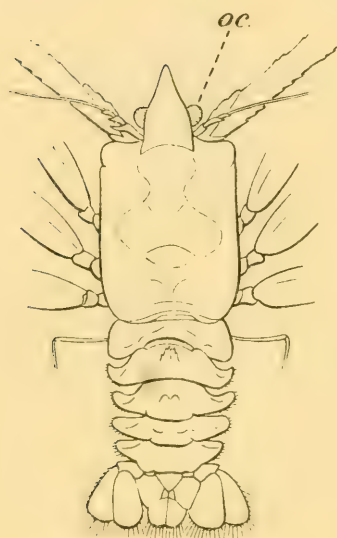


FIG. 9.

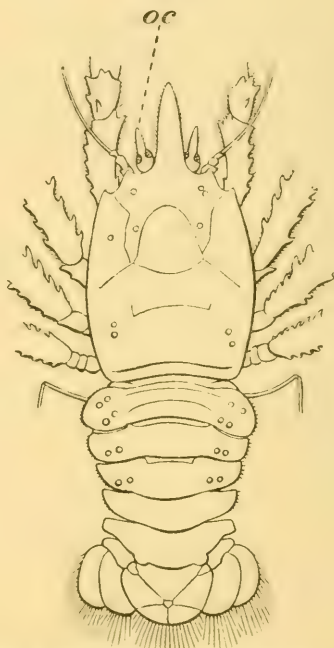


FIG. 8.—*Munidopsis carinipes*, Fax. 695 fathoms. Eyes normal. "Challenger" Reports: 'Stalk-eyed Crustacea,' pl. xxiv, fig. 1.

FIG. 9.—*Munidopsis Hendersoniana*, Fax. 1020 fathoms. The corneal area is reduced and divided, and the ocular peduncle projects beyond it as a rostrum. 'Stalk-eyed Crustacea,' pl. xxiv, fig. 2.

Association Report of that year, and in Sir Wyville Thomson's 'Depths of the Sea.' The figures which occupy our Pls. 33 and 34 were drawn twenty-eight years ago for Dr. Norman by his friend, the eminent naturalist and artist, Albany Hancock.

The original account of *Ethusa* (*Cymonomus*) *granulata* by Norman is given in Sir Wyville Thomson's 'The Depths of the Sea,' 1873, p. 176. He there writes—I

quote from a preliminary notice of the Crustacea by the Rev. A. Merle Norman—"Ethusa granulata (sp. n.), the same species as that found off Valentia, but exhibiting a most extraordinary modification of structure. The examples taken at 110—370 fathoms in the more southern habitat have the carapace furnished in front with a spinose rostrum of considerable length. The animal is apparently blind, but has two remarkable spiny eye-stalks, with a smooth rounded termination where the eye itself is ordinarily situated. In the specimens, however, from the north, which live in 542 and 705 fathoms, the eye-stalks are no longer movable. They have become firmly fixed in their sockets, and their character is quite changed. They are of much larger size, approach nearer to each other at their base, and, instead of being rounded at their apices, they terminate in a strong rostrate point. No longer used as eyes, they now assume the functions of a rostrum; while the true rostrum, so conspicuous in the southern specimens, has, marvellous to state, become absorbed. Had there been only a single example of this form procured, we should at once have concluded that we had found a monstrosity; but there is no room for such an hypothesis by which to escape from this most strange instance of modification of structure under altered conditions of life. Three specimens were procured on two different occasions, and they are in all respects similar."

The specimens thus described are those now before me—forming part of the Norman Collection acquired by the trustees of the British Museum. They have, until now, not been figured or further described, and are therefore practically unknown to carcinologists. They are preserved in alcohol in separate tubes, labelled as follows:

a. "Porcupine, 1869; Stations 24, 29, 30; 109 to 1380 fathoms. Between Ireland and Rockall." [These are two specimens of normal form as drawn in Pl. 33, fig. 2, of the present memoir.—E. R. L.]

b. "Off Cape St. Vincent, Station 25; Porcupine, 1870; 374 fathoms." [One specimen of normal form.—E. R. L.]

c. "Porcupine, 1869; Stations 1, 2, 3, 8; 106—808 fathoms. Off S.W. Ireland." [Seven specimens of normal form.—E. R. L.]

d. "Holtenia ground, Porcupine, 1869; Stations 47*a* and 88; 542 and 705 fathoms."

[Three specimens of the form with modified eye-stalks and rostrum (see Pl. 34, figs. 8, 10, 11). These are the specimens referred to by Canon Norman in the extract above given from 'The Depths of the Sea,' and appear to be the only specimens of this form hitherto found. It seems important to point out at once that, so far as actual depth is concerned, the extreme depth of the stations in which the normal specimens were found exceeds that at which the modified form from the *Holtenia* ground was procured. Female specimens show a length of 4 mm. from the posterior margin of the carapace to the base of the rostrum; male specimens are as small as 2.4 mm. in the same dimension.—E. R. L.]

It will be obvious at once that Dr. Norman only described two forms of his *Ethusa granulata*—both of them blind; but whilst the one still retained a corneal area on the eye peduncle, the second form had lost this character, and the eye-stalks had become immovable and more or less pointed (see Pls. 33 and 34).

It is, therefore, remarkable that Lord Avebury should speak in the paragraph cited at the commencement of this memoir of three forms, adding a form "living near the surface" and having "well-developed eyes." This third form has not yet been discovered in the genus *Cymonomus*, but Lord Avebury is quite right in principle, since there is no doubt that such a shallow-water form has existed, and very possibly still exists. In other genera closely allied to *Cymonomus*—for instance, in *Cyclodorippe uncifera*, Ortm.—a form from a depth of fifty metres is described (Doflein, 'Biol. Centralblatt,' August, 1903) with well-pigmented eyes and longer eye-stalks; whilst in specimens of the same species from a depth of 700 metres

the pigment is feebly developed, the ommatidia few and incompletely developed, and the eye-stalk short. Thus Cyclo-dorippe completes the eye-series of Cymonomus, and like the less closely related Bathyplox cited at the end of Dr. Ortman's list, justifies in large measure Lord Avebury's supposition of a Cymonomus-form living in shallow water and having well-developed eyes.

Dr. Norman's very brief account of *Ethusa* (*Cymonomus*) *granulata*, which he intended to supplement by further publication many years ago, has led to some misapprehensions. In the first place it cannot be maintained, on considering the facts recorded as to depth at which the specimens were taken, that the more modified form is correlated with origin from deeper water. Normal specimens occur at 808 fathoms, and even at 1380 fathoms, whilst the peculiar forms with rostriform eye-stalks occur at 542 fathoms. It seems to be of greater significance that the locality in which the latter were found is what Wyville Thomson and Carpenter called "the Holtenia ground." This fact may perhaps be brought into relation with the discovery by the eminent carcinologist Dr. Hansen of a similarly modified *Cymonomus* among the Crustacea dredged by the "Ingolf" around Greenland and Iceland and north and west of the Faroe Islands. Dr. Hansen has been good enough to communicate this fact to me, and a drawing¹ of the single specimen obtained. It was taken at a depth of 486 fathoms (bottom temp. 5.5° C.) in lat. N. $62^{\circ} 58'$, long. W. $23^{\circ} 28'$.

I am, therefore, inclined to regard Dr. Norman's form with rostriform eye-peduncles as having a geographical and not merely a bathymetrical correlation.

I may further remark that Dr. Norman's words as to the modification of the eye-stalks in his deeper water form have been misunderstood by subsequent writers. He says "they terminate in a strongly rostrate point. No longer used as eyes, they now assume the functions of a rostrum." This has

¹ See text-figure 12.

led, naturally enough, to the interpretation that "their terminations become combined into a strong pointed beak." But Dr. Norman's intention was to describe each eye peduncle as converted into a separate rostrum, the points of which do not combine, but diverge widely from one another (see figures in Pls. 33 and 34).

I now pass on to a brief statement of the foundation of the genus *Cymonomus* by Alphonse Milne-Edwards for a West Indian crab, his *C. quadratus*, and the subsequent discovery of Norman's normal form of *Ethusa granulata* (not the form with rostral eye-stalks) by the French naturalists in the Mediterranean, and the reference by Milne-Edwards of this *Ethusa* to his genus *Cymonomus*.

It was in 1880 that Alphonse Milne-Edwards established the genus *Cymonomus* in the 'Report on the Results of Dredging by the United States Coast Survey steamer "Blake;"' viii, "Études préliminaires sur les Crustacés," 1re partie, p. 26.

He writes, "*Cymonomus* (nov. gen.): La carapace est étroite et terminé en avant par un rostre pointu de chaque côté duquel s'insèrent les pédoncules oculaires grêles, de grosseur uniforme et dépourvus de corneules. Les antennes internes sont grandes et ne peuvent se replier sous le front. Les antennes externes prennent naissance au dessous et en dehors des antennules, et elles sont notablement plus courtes qu'elles: le tubercule auditif se développe en une saillie spiniforme. Le cadre buccal porte en avant, sur la ligne médiane, une large échancrure; il est entièrement caché par les pattes machoires qui s'avancent beaucoup de manière à recouvrir la base des antennes. L'exognathe est très allongé; le mérognathe est étroit, et son extrémité débord de beaucoup le peu [sic] d'insertion du palpe. Les pattes antérieures sont courtes et terminées par les doigts pointus. Les pattes de la 2e et de la 3e paire ressemblent à celles du *Cyclodorippe*, celles de la 4e et 5e paire sont très petites relevées sur le dos et terminées par un petit ongle crochu, mais elles ne sont pas cheliformes. L'abdomen du mâle est

très court. Le dernier article de l'abdomen de la femelle est triangulaire et arrondi à son extrémité. Les œufs sont très gros et en petit nombre. Les orifices génitaux de la femelle s'ouvrent sur l'article basilaire des pattes de la 3e paire."

The species assigned by Milne-Edwards to this new genus is *C. quadratus*, n. sp., from the West Indies, taken at depths ranging from 175 to 500 fathoms.

No figure was at this time published of *C. quadratus*, the fuller publication of the "Blake" Crustacea being deferred, and subsequently accomplished (as noted below) by Prof. Bouvier in collaboration with Prof. Milne-Edwards.

In 1881 M. Milne-Edwards, in a summary account of some dredging operations made in the Mediterranean ('Comptes Rendus Acad. Sci.,' Paris, xciii, p. 879), refers to Norman's species as "*Cymonomus* (*Ethusa*) *granulatus* (Norman)," and records it as occurring in a new locality, viz. the Mediterranean. No figure was at this time in existence of any *Cymonomus*, but in 1883 *C. granulatus*, Norman, appears in the 'Recueil de figures des Crustacées nouveaux ou peu connus,' produced by M. Alphonse Milne-Edwards, and, as I believe, privately distributed. This was the first occasion on which a figure of *C. granulatus*, or indeed of any *Cymonomus*, was published.

The drawings on this plate are reproduced in pl. xi of the 'Expéditions scientifiques du "Travailleur" et du "Talisman:" Crustacées Décapodes, par A. Milne-Edwards et E. L. Bouvier,' published in 1900. A drawing showing the frontal region of the carapace from below, with the eye-stalks, antennules, and antennæ in position, has been re-executed, but the large figure of the whole animal, seen from the dorsal surface, is reproduced without modification. This is in some ways to be regretted, since the eye peduncles have been removed from the specimen before it was given to the artist for portraiture, and consequently two cavernous, deeply shaded areas are represented, one on each side of the frontal rostrum, between it and the large extra-orbital spine. The fact that the specimen is incomplete is not mentioned in the explana-

tion of the plate, and though obvious to the carcinologist has led to some misunderstanding. Thus in the excellent volume 'La vie au fond des Mers,' by the late Professor Filhol, a woodcut of this mutilated specimen is given as representing the species concerning the eye-stalks of which Dr. Norman's observations are quoted in full, although the figure shows no eye-stalks at all!

The drawing made by Mr. Albany Hancock in 1875, and now published as fig. 2 in Pl. 33 of the present memoir, really represents accurately the normal *C. granulatus* of Norman as it actually appears; and it will be seen, if this drawing be compared with those given in the earlier publications, that there are important deficiencies in the latter. Having carefully compared the type specimens of Norman now in the British Museum (Natural History) with Mr. Hancock's drawings, I have satisfied myself that they could not be improved upon, and have therefore reproduced them untouched. Those who have already learnt to know the accuracy and artistic ability of that admirable naturalist will not be surprised that this course has been followed.

With regard to the other species of *Cymonomus*, the *C. quadratus* for which Milne-Edwards established the genus, no figure was published until the year 1902, when in the 'Memoirs of the Museum of Comparative Zoology at Harvard College,' vol. xxvii, No. 1, MM. Milne-Edwards and Bouvier published their account of the crabs of the families Dromiacea and Oxytoma, dredged by the U.S. Coast Survey steamer "Blake."

The genus *Cymonomus* is there described by MM. Milne-Edwards and Bouvier as forming with the genera *Palicus*, *Ethusa*, *Cymopolus*, *Corycodus*, *Clythrocerus*, and *Cyclodorippe*, the family Dorippidae, M.-Edw.

Two species of *Cymonomus* are described, viz. *C. quadratus*, M.-Edw., the type species, and *C. granulatus*, Norman. A plate (pl. xvi) is given to the illustration of *C. quadratus*, which, although described at an earlier date by Milne-Edwards, was not figured when that author published his figure of *C. granulatus* in the "Travailleur" volume.

The drawing of a dorsal view of the complete *C. quadratus* given in fig. 1 of this plate shows a form which is closely related to *C. granulatus*, Norm., but with well-marked, distinct specific character. A very astonishing feature, however, is represented in the figure, namely, the two posterior pairs of thoracic limbs are pictured as being chelate, as in some *Dromiidae*. This feature would necessitate the complete generic separation of *C. quadratus* from *C. granulatus*; and as this remarkable condition of the hinder thoracic limbs is not mentioned in the text, and in the earlier description of the genus by M. Milne-Edwards is expressly denied, I felt sure that by a curious oversight the artist had figured the hinder limbs of a *Dromiid* in place of those of the actual specimen of *Cymonomus* which he had set out to draw. Such a confusion of specimens by the artist, and the subsequent escape of the error from detection by the zoologist for whom the drawings have been made, is a possible psychological phenomenon, and is comparable to a revoke in the game of whist when a card in the player's hand escapes his observation, although he is looking at it, and knows that he must play such a card if he have it.

I accordingly wrote to my friend Professor Bouvier, the distinguished naturalist in charge of the collections of Arthropoda in the Muséum d'Histoire Naturelle of Paris, and he has informed me that he is utterly astonished to find the figure as it is, in spite of the fact that this and all the other plates were carefully revised by him. He states that the fourth and fifth thoracic pairs of limbs of *C. quadratus* are not chelate, but resemble those of *C. granulatus*. At the same time he was kind enough to send me some of the type specimens of *C. quadratus* for examination, which show the hinder limbs in place and of the usual form. He was also so good as to send me specimens of *C. granulatus* from the Mediterranean for comparison with Norman's types.

We are now in a position to deal more definitely with Dr. Norman's original specimens of *C. granulatus*.

In the first place it is to be noted that M. Milne-Edwards

has expressly stated that he has not received any specimens corresponding to Norman's aberrant form with rostriform immobile eye peduncles and aborted rostrum. His specimens were dredged off Porto, Gibraltar, Villefranche, Marseilles, and Ajaccio. He says ('Travailleur,' p. 39), " Dans tous les spécimens que nous avons étudiés, et ils sont nombreux, les pédoncles oculaires sont mobiles, la surface cornéenne est lisse et parfois même un peu colorée, le rostre en outre est très saillant. Comme ces spécimens habitent des profondeurs très variables (de 300 à 350 mètres), on peut conclure que la transformation des yeux en pointes rostrales [resp. Norman's aberrant specimens—E. R. L.] est fonction, non point de la distribution bathymétrique, mais de la distribution géographique. Les exemplaires du nord, en d'autres termes, présenteraient seuls cette transformation."

I think it will be most convenient, as well as logical, to regard Norman's aberrant form as a distinct species, to which I shall give the name *C. Normani*. It appears from a reference to MS. in the "Travailleur" report that Dr. Norman himself had contemplated treating this form as a distinct species under the name *Ethusa mirabilis*. I should adopt the name so long ago suggested by my friend were it not for the fact that it seems possible that there may be other forms—terms in the series—allied to *C. granulatus* and *C. Normani*, and that it will be convenient to associate the name of each form so far as possible with some person or thing distinctive of its discovery.

The position and characters of the three species of *Cymonemus* may accordingly be thus given:

Section OXYSTOMA, M.-Edw. (of the *Brachyura genuina*, Boas).

Family Dorippidæ, M.-Edw., including sub-families Cyclo-dorippinæ and Dorippinæ.¹

¹ The characters of these divisions and the included genera are very fully given by MM. Edwards and Bouvier in the "Blake" volume quoted above.

Sub-family Cyclodorippinæ, including two tribes, Cymonomæ (genera *Cymopolus* and *Cymonomus*) ; Cyclodorippæ (genera *Corycodus*, *Clythocerus*, *Cyclodorippa*, and *Cymonomops*).

Tribe Cymonomæ.

Characters (taken from Edwards and Bouvier).—Carapace quadrate, rugose ; rostrum somewhat narrow, triangular, with pointed termination. Afferent orifices very much reduced or rudimentary. Efferent orifices more or less separate, and situated far behind the frontal margin. Exopodite of the first maxillipedes more developed than their external lacinia ; that of the second maxillipedes quite normal. An exopodial flagellum and a reduced or rudimentary epipodite present on the third maxillipedes. Probably always three pairs of swimmerets in the female.

Genus *Cymonomus*, A. M.-Edw., 1880.

Characters (as given by Edwards and Bouvier).—Efferent orifices very far separate from one another, and situate at the base of the antennæ. External lacinia of the first maxillipedes much shorter than the base of the exopodite. Second maxillipedes with a rudimentary epipodite, but without any branchiæ. Third maxillipedes with reduced epipodite, dilated and articulated at its base, with the mesopodite standing forward and carrying the carpus on its internal face. A single pleurobranch : three pairs of swimmerets in the female. Blind. The antennæ cannot conceal themselves completely beneath the rostrum (in *Cymopolus* they can).

Species 1.—*C. quadratus*, A. Milne-Edwards. ‘Bull. Mus. Comp. Zool.’ vol. viii, No. 1, p. 26 (1880).

The characters which distinguish this species from *C. granulatus* are stated by M. M.-Edwards and Bouvier as follows :

1. All the parts of the body are less granular and much

less richly furnished with hairs; these latter notably are not present on the dorsal face of the carapace.

2. The cervical groove is much more marked in *C. quadratus*, but the branchial region is less so, and in fact presents no distinct limit anteriorly.

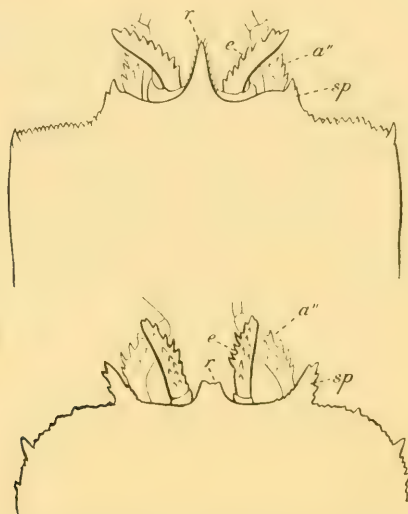


FIG. 10.—Outline diagrams of the anterior margin of the carapace, the rostrum, and ocular peduncles of two specimens of *Cymonomus quadratus*, M.-Edw. The upper figure is taken from M. Milne-Edwards' figure in the "Travailleur" volume, and the lower is drawn from a specimen kindly communicated by M. Bouvier. Both figures show the peculiar form of the ocular peduncles, *e*, differing both from those of *C. granulatus* and *C. Normani*; also the proportionate size of the rostrum, *r*. The lower figure shows a greater size attained by the extra-orbital spines, *sp*, and a rounding off of the lateral angles of the carapace, as compared with the type.

3. The rostral region¹ is less pronounced, and advances less distinctly in front of the carapace; the rostrum is much narrower, and has no denticles on its margins.

4. The ocular peduncles are much more delicate, and are gradually attenuated from the base to the summit; their

¹ See our text block, Fig. 10, *r*, and compare with Pl. 33, fig. 2.

corneal surface is no longer distinct as in *C. granulatus*, and numerous spinules are grouped in a row on the internal border of the peduncles.¹

5. The second joint of the antennary peduncles, instead of being delicate and almost smooth as we see in *C. granulatus*, is much larger than the others, and possesses spines on its external border.²

6. The notch of the palatine border is less extensive than in *C. granulatus*, so that the two halves of the border pass considerably to the inner side of the urinary tubercle. On the contrary, the palatine surface is complete in *C. granulatus*, whilst presenting on each side a small antero-posterior crest.

7. The base of the exopodite of the first and second maxillipedes advances less in front than in *C. granulatus* [*quadratus* in original—E. R. L.].

8. The last abdominal segment of the female has regularly rounded-off side borders in *C. granulatus*; whilst in *C. quadratus*, on the contrary, the border on each side forms an inwardly convex curvature.

Distribution.—*C. quadratus* represents in the Caribbean region the *C. granulatus* of the Mediterranean and North Atlantic.

Species 2.—*C. granulatus*, Norman. 'Brit. Assoc. Reports' (as *Ethusa granulata*), 1873.

In addition to the definite points of difference between this species and *C. quadratus* quoted above from M. M. Edwards and Bouvier may be mentioned the generally more granular condition of the surface, and the tendency to an

¹ See our text block, Fig. 10, *e*, and compare with Pls. 33 and 34.

² See Pl. 34, fig. 12. The joint referred to is what appears in the drawing as the first or proximal, the true first being fused with and hidden beneath the carapace. The observation as to the difference of the spinulation of this joint in *C. granulatus* and *C. quadratus* is confirmed by the examination of our specimens in the Nat. Hist. Mus. But *C. Normani* has as spinose a margin to the joint as *C. quadratus*, and has the next joint also spiniferous, although it is quite smooth in *C. granulatus* (see p. 457).

exuberance in the production of spines and spinules, which exhibits individual variation.

As stated by M. M.-Edwards and Bouvier, *C. granulatus* is more richly beset with fine hairs than is *C. quadratus*. These hairs are not represented in Mr. Albany Hancock's drawings reproduced in our plates, but are present in Norman's specimens both on the eye peduncles and other appendages as well as on the carapace.

The difference in the form of the eye-stalks is very striking—those of *C. granulatus* presenting a well-marked corneal area which is absent from those of *C. quadratus*, and also being more robust, rounded in cross-section instead of flattened, and beset with numerous spinules. The row of spines on the inner margin is not so regular as in *C. quadratus* (see Pl. 33, figs. 5 and 6). The rostrum also is larger and more robust, and provided with coarser spinules in *C. granulatus* than in *C. quadratus*, and projects considerably further forward than the eye-stalks, whereas in *C. quadratus* it is not so long as the eye-stalks.

In both species there is a well-developed extra-orbital spine on the frontal margin of the carapace on each side (Pl. 34, fig. 7, *sp.*, and text-fig. 10, *sp.*). But this spine is much larger and more coarsely denticulate in *C. granulatus* than in *C. quadratus*. It appears to be subject to variation in *C. quadratus*, as it is larger in the lower specimen drawn in our text-fig. 10 than in the upper, which is taken from the figure of M. M.-Edwards and Bouvier. It seems to me that the prominence and great size of this extra-orbital spine, forming with the base of the rostrum an almost cup-like cavity on each side of that structure, as shown in A. Milne-Edwards' drawing of a mutilated specimen devoid of eye peduncles ('Travailleur,' loc. cit., pl. xi, fig. 5), is eminently characteristic of *C. granulatus* as compared with *C. quadratus*.

Distribution.—Mediterranean and North Atlantic.

Species 3.—*Cymonomus Normani*, n. sp. (1903).

As *C. granulatus* in all characters except the following.

The rostrum is reduced to a small process in the mid-frontal line (see Pl. 34, fig. 8): two other forms of the diminutive rostrum are seen in Pl. 34, figs. 10 and 11, thus necessitating the emendation of the character as to the size and form of the rostrum by which the tribe Cyclodorippæ were supposed to be separated from the tribe of the Cymonomæ.

The ocular peduncles of *C. Normani* have moved from the lateral position which they occupy in *C. granulatus*, and approach the middle line from each side. Their bases are actually fused to one another beneath the rudimentary rostrum, and they are immovably united to the margin of the carapace (see Pl. 39, fig. 8). Further, the free diverging¹ stems of the ocular peduncles differ greatly in form from those of *C. granulatus*. Like those of *C. quadratus*, they are entirely devoid of a corneal area, and taper gradually to the extremity. But, unlike those of *C. quadratus*, the ocular peduncles of *C. Normani* are not straight, and denticulate on the inner face only. They present, on the contrary, a curvature, first inwards, then outwards, and then again strongly inwards at the extremity (Pl. 34, fig. 10). They are very much more richly beset with spinules than are the ocular peduncles of *C. granulatus*, and the spinules are of larger size.

Speaking generally, the spinules on the frontal region of the carapace, extra-orbital spines, basal antennary joints, and eye peduncles are coarser and more exuberant in *C. Normani* than in *C. granulatus*. As shown in Pl. 34, fig. 8, the theoretical third (the actual second) joint of the antennary peduncle, *a''*, is fringed externally with spines in *C. Normani*; these are wanting in *C. granulatus* (Pl. 34, fig. 7, *a''*).

Distribution.—Only three specimens of this species are known, viz. those originally dredged by the Rev. Canon Norman on the Holtenia ground in 1869 in the cruise of the "Porcupine."

¹ Not united to form a single rostrum as Dr. Norman's brief description had led some of his readers to suppose.

Since the present memoir was completed my attention has been drawn to an article in the 'Biolog. Centralblatt,' August, 1903, written by Mr. F. Doflein, on "The Eyes of Deep Sea Crabs." The article contains interesting observations on the microscopic structure of the more or less degenerate eyes of certain species. I have already inserted above a reference to Mr. Doflein's description of the more and the less degenerate condition of the ommatidia in specimens of *Cyclo-dorippe uncifera* from deeper and shallower waters. Mr. Doflein makes some remarks upon *Cymonomus granulatus*, Norm., of which he figures an eye peduncle taken

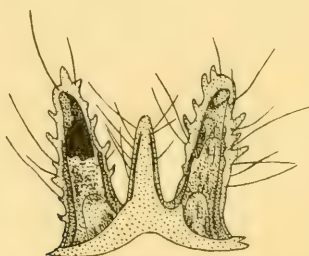


FIG. 11.—Rostrum and eye peduncles of a species of *Cymonomus*, dredged by the "Valdivia" off the east coast of Africa. Reproduced from Doflein.

from a Mediterranean specimen communicated to him by Prof. Bouvier. He also gives a drawing, reproduced here (text-fig. 11), of the rostrum and ocular peduncles of a *Cymonomus* taken (a single example) on the East African coast by the Valdivia Expedition at a depth of 1000 metres. Mr. Doflein refers this specimen to *Cymonomus granulatus*, and considers it to be a form of that species with degenerate eyes.

It seems to me, from the drawing given and here reproduced, that this East African *Cymonomus* is much nearer to *Cymonomus quadratus* than it is to *C. granulatus*. The ocular peduncles are in the condition which is normal and typical in *C. quadratus*, whilst the rostrum is relatively little shorter than in that species (conf.

text-fig. 11). On the other hand, the long and somewhat coarse hairs on both eye-stalks and rostrum seem to distinguish this species from *C. quadratus*. It certainly is not likely that this East African form should be identical with the Mediterranean and North Atlantic *C. granulatus*. I think that it will prove to be either a hairy variety of *C. quadratus* or a sufficiently distinct form to be entitled to a specific name, in which case I propose to speak of it as *Cymonomus Valdiviæ*.

Still more recently I have received a most interesting

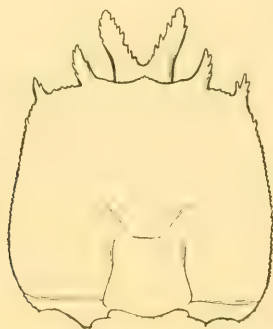


FIG. 12.—Outline diagram from Dr. Hansen's drawing of the "Ingolf" specimen of *Cymonomus* allied to *C. Normani*.

communication from my friend Dr. Hansen, of Copenhagen, relative to a *Cymonomus* dredged by the Ingolf Expedition in lat. N. $62^{\circ} 58'$, long. W. $23^{\circ} 28'$, at a depth of 486 fathoms, to which I have already referred above.

Dr. Hansen has been kind enough to send me an excellent drawing of the dorsal view of the remarkable "Ingolf" specimen. He will himself describe it hereafter in full, but I may say here that it is most distinctly a further term in the development of those special features which distinguish *C. Normani* from *C. granulatus*. In the Ingolf's *Cymonomus* the rostrum, as shown in the outline here given (text-fig. 12), is not even represented by a trifid spine; it is reduced to a scarcely prominent process of the margin of the carapace.

The extra-orbital spines are larger than in *C. Normani*, and the spines at the latero-frontal angles of the quadrate carapace are emphasised. The eye peduncles seem to be straighter and stronger than in *C. Normani*, and more broadly united to one another at the base.

I am not able to speak with any certainty on the next point, but if I may judge by Dr. Hansen's drawing the *Ingolf's* *Cymonomus* is less generally beset with spinules, and these are less prominent than is the case with *C. Normani*. In this respect the "*Ingolf*" form appears not to carry on the distinctive characters of *C. Normani* in an exaggerated degree. But we shall no doubt receive fuller information on the subject from Dr. Hansen.

It is worth noting by the way that degrees of degeneration of the eyes are known in the genus *Cymopolus*, M.-Edw., as well as in the allied genus *Cymonomus*.

Cymopolus Agassizii, M.-Edw., has the corneal surface very greatly reduced, and there is an absence of pigment; whilst in *Cymopolus asper*, M.-Edw., the corneal area of moderate size is strongly pigmented with black.

Apparently *Cymonomus quadratus* is the only member of the *Cyclodorippine* crabs (or of any *Brachyurous* group except *Bathyplox*) which has hitherto been described as having the corneal area completely absent, and the ocular peduncle persisting as a mere pointed rod. *C. Normani* is now added to that list, as well as the forms dredged by the "*Valdivia*" and the "*Ingolf*."

NOTE BY DR. A. M. NORMAN, F.R.S.

The range of the described members of the genus *Cymonomus* is as follows:

1. *Cymonomus Normani*, E. Ray Lankester.

"*Porcupine*," 1869. Lat. $59^{\circ} 34' N.$, long. $7^{\circ} 15' W.$, 542 fathoms; and lat. $59^{\circ} 26'$, long. $8^{\circ} 23'$, 705 fathoms. These dredgings are to the north-west of the Butt of Lewis, and in the

“warm area” to the south of the “Wyville-Thomson Ridge.”

2. *Cymonomus granulatus*, Norman.

a. In many “Porcupine” dredgings in 1869 off the west and south-west of Ireland, in 106—1350 fathoms.

b. Off the coasts of Spain and Portugal, dredged by the “Porcupine,” 1870, “Travailleur,” “Talisman,” and “Hirondelle.”

c. Northern Mediterranean, off the south of France and off Corsica, “Travailleur,” 1881. Southern Mediterranean, “Porcupine,” 1870; Station 56; lat. $37^{\circ} 3' N.$, long. $11^{\circ} 36' E.$, that is near the island Pantellaria, between Tunis and Sicily, in 390 fathoms.

d. African coast. Taken by the “Talisman” more than twenty degrees south of the Mediterranean, off Arguin, lat. $21^{\circ} 53' N.$, in 655 metres.

3. *Cymonomus quadratus*, A. Milne-Edwards, 1880.

Among the West Indian islands, in 175—508 fathoms.

The number of species of Crustacea Brachyura rapidly diminishes as we descend in our investigations into the depths of the ocean; and it is worthy of notice here that the only species, I believe, which have as yet been found in depths exceeding 1000 fathoms belong to genera allied to *Cymonomus*, as will be seen in the following list.

Cymonomus granulatus (Norman), as

above 1380 fathoms.

Ethusa microphthalma, S. I. Smith.

U.S. Fish Comm. dredgings, 1884 . 1047 „

“Challenger” 1000 „

Ethusina abyssicola, S. I. Smith.

“Albatross,” 1883, Atlantic . 1497—1735 „

“Talisman” 4060 metres.

Ethusina Challengeri, E. I. Miers.

"Challenger" 1875 fathoms.

"Albatross," Pacific 2232 "

Ethusina gracilipes, E. I. Miers.

"Challenger" 1425 "

"Albatross," Pacific 1322—1823 "

Ethusina Talismani, E. Milne-Edwards and Bouvier.

"Talisman" 2235 metres.

"Princesse-Alice," 1897 1935 "

EXPLANATION OF PLATES 33 & 34,

Illustrating Prof. Ray Lankester's memoir on
"The Eye Peduncles of *Cymonomus*."

Reference Letters.

a' = Antennule. a^* = Basal articulation of same. a'' = Antenna. e = Eye-stalk (ocular peduncle). r = Rostrum. sp = Extra-orbital spine or process of the carapace. x = Small scale, probably an abnormality.

FIG. 1.—*Cymonomus Normani*, n. sp. Male specimen, showing the modified rostrum and eye-stalks.

FIG. 2.—*Cymonomus granulatus*, Norman. Male specimen, showing the normal rostrum and eye-stalks.

FIG. 3.—Abdomen of male *C. granulatus*.

FIG. 4.—Abdomen of female *C. granulatus*.

FIGS. 5 and 6.—Eye-stalks of *C. granulatus*.

FIG. 7.—Frontal region of *C. granulatus* further enlarged.

FIG. 8.—Frontal region of *C. Normani* further enlarged.

FIG. 9.—Maxillipede of third pair of *C. granulatus*.

FIG. 10.—Eye-stalks and rostrum of a female specimen of *C. Normani*.

FIG. 11.—Eye-stalk and rostrum of a second male specimen of *C. Normani*.

FIG. 12.—Antennule and antenna of *C. granulatus*.

FIG. 13.—Part of antennule of *C. granulatus* further enlarged.

The following remarks in reference to these drawings and the original specimens are kindly furnished by Dr. W. T. Calman, who is now engaged on carcinological work in the Natural History Museum.

"The specimen represented in Figs. 1 and 8 is a male, the carapace of which measures about 3.4 mm. in length to the base of the rostral process. Fig. 10 is taken from a female specimen with carapace 4 mm. in length, and Fig. 11 from a male 2.4 mm. in length.

"The originals of the other figures cannot now be identified.

"In the specimen shown in Figs. 1 and 8 the eye-stalks are not quite so near together at the base as in the figure, though they are somewhat nearer than in the specimens from which Figs. 10 and 11 have been drawn. One of these (Fig. 10) has at the tip of the eye-stalks a slight trace of the brownish coloration which in normal specimens distinguishes the corneal area, but this cannot be discerned in either of the other two specimens.

"Fig. 12 shows a small scale (*x*) apparently articulating with the end of the proximal joint of the antennal peduncle. This appears to be exceptional in occurrence, and is not present in the specimens examined by me. It seems to be a development of the primitive third joint of the peduncle, usually fused with the second and indicated only by a sutural line.—W. T. C."

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CONTENTS OF No. 188.—New Series.

MEMOIRS:

	PAGE
On the Dermal Fin-rays of Fishes—Living and Extinct. By EDWIN S. GOODRICH, M.A., Fellow of Merton College, Oxford. (With Plates 35—41)	465
The Structure and Classification of the Arthropoda. By E. RAY LANKESTER, M.A., LL.D., F.R.S., Director of the Natural History Departments of the British Museum. (With Plate 42)	523
Some Problems of Reproduction.—II. By Professor MARCUS HARTOG, Queen's College, Cork	581

On the Dermal Fin-rays of Fishes—Living and Extinct.

By

Edwin S. Goodrich, M.A.,

Fellow of Merton College, Oxford.

With Plates 35—41.

CONTENTS.

	PAGE
INTRODUCTION	466
THE DERMAL RAYS OF LIVING FISH	468
Elasmobranchii	468
Holocephali	471
Teleostei	471
Amia	477
Lepidosteus	477
Polypterus	478
Acipenser	479
Dipnoi	480
THE STRUCTURE AND HOMOLOGIES OF THESE DERMAL RAYS	483
THE DERMAL RAYS OF FOSSIL FISH	492
Elasmobranchii	492
Acanthodii	492
Ichthyotomi	493
Ostracodermi	493
Arthrodira (Coccosteus)	494
Actinopterygii	494
Isospondyli	494
Protospondyli	495
Ætheospondyli	495
Chondrostei	495

	PAGE
Crossopterygii	499
Osteolepidæ	499
Glyptopomidæ	500
Rhizodontidæ	500
Holoptychiidæ	501
Cœlacanthidæ	502
Dipnoi	503
CONCLUSION	512

INTRODUCTION.

IN the following paper are given the results of a study, carried on for some years, on the structure and development of the dermal fin-rays of fish. The classification of living and extinct fish is a subject which has grown much in importance of late years, and has been greatly advanced in quite modern times through the labours of Cope, Traquair, A. Smith Woodward, and others. Almost every available character has been made use of in turn by systematists in the endeavour to classify the larger groups; and of these characters it is obvious that those which are based on structures capable of being fossilised must be the most useful. No parts of a fish are, as a rule, better preserved than the dermal skeleton. Yet, although Agassiz (1) long ago classified fish into large divisions according to the structure of the scales, modern systematists are inclined to attach so little importance to the exo-skeleton that I venture to think they have somewhat neglected the dermal fin-rays. If it is true that the application of cut and dried definitions of the scaling will no longer enable us satisfactorily to subdivide the Pisces into Placoidæi, Ganoidei, Cycloidei, and Ctenoidei; if it is true that "placoid" scales may be present in the Ganoidei, and that various forms of cycloid scales may have been independently evolved from rhomboid ganoid scales in later groups,—nevertheless these facts do not by any means prove that the scaling is of little systematic importance.

Indeed, are there any characters against which the same objections may not be urged ?

Paradoxical as it may seem, yet the most superficial structures are often of the deepest significance in the study of phylogeny. As a mammal may be surely identified by its hair, and a bird by its feather, so may a fish be classified by its dermal fin-ray. The dermal rays, however, are of even more constant structure than the body-scales. There seem to be only three main types of these rays, and it was with the object of defining these types, and of tracing out their phylogenetic relations, that this work was undertaken, in the hope of thereby helping to clear up some obscure points in classification. Unfortunately the task has proved far less easy than I expected, chiefly on account of the many difficulties encountered in the study of fossil forms. The work remains incomplete; many important questions are left undecided; yet I hope enough has been done to show that it is a fruitful field for research, from which much may be expected.

The bulk of this work was carried out on the material in the Department of Comparative Anatomy of the Oxford Museum. I have to thank Professor Sollas for the loan of specimens from the Geological Department, and Professor Zittel for permission to freely examine the famous Munich collections. More especially I am indebted to Dr. R. H. Traquair and Dr. A. Smith Woodward for much help and advice whilst working through the collections in the Edinburgh and British Museums.

The dermal rays of fish have already been described in considerable detail by many authors. In the first half of the nineteenth century Agassiz, in his classical memoir (1), mentioned the bony and generally jointed rays of the higher fish, and the unjointed horny rays of the Selachians and Chimæra. He also described the slender horny rays in the embryonic fins of Teleostean fish, and the dermal rays of many fossil forms. Bruch in 1861 (5) first drew a clear distinction between the endo-skeletal rays and the secondary

rays belonging to the dermal skeleton. O. Hertwig, in a series of most important papers on the dermal skeleton of fish (17), contributed numerous observations on the structure and development of the rays, and clearly established the homology of the jointed bony rays of the Actinopterygii with the body-scales. Beaudelot (2) had previously put forward the same view, and had given a clear general account of the development of the dermal rays in Teleosts, which subject has again been most successfully studied in detail by Harrison (13). An interesting general discussion of the dermal rays has been published by Ryder (32), in which he upholds the view that they are homologous throughout all the groups of fish in which they occur. Pander (27 and 28), Traquair (35, 36, 37), A. Smith Woodward (42), and others have from time to time contributed many important observations on the fin-rays of extinct forms.

Before describing the dermal fin-rays of the true Fish, it may be mentioned that real dermal rays are absent in *Amphioxus* and the Cyclostomes. The ray-like structures figured and described by various authors in the larva of *Amphioxus* (Hatschek [16], Lankester and Willey [23]) are elongated epidermal cells. They have nothing to do with the dermal rays of fish. In the Cyclostomes, on the other hand, the fins are supported by delicate cartilaginous rays, prolongations of the neural and hæmal arches of the axial endoskeleton.¹

Elasmobranchii.

It is well known that the fins of the Elasmobranch fish, whether paired or unpaired, are provided with so-called "horny fin-rays." These rays are slender, flexible, cylindrical rods of fibrous substance, deposited in concentric layers. They are pointed at the proximal end, and gradually diminish

¹ Dermal rays are figured by mistake in the adult *Bolellostoma* by B. Dean (8). It would be interesting to know whether there are any traces of such rays in the young.

in diameter towards the distal extremity. The horny fin-rays—which I shall call the *ceratotrichia*—never become ossified, and are never jointed. Moreover, as a rule, they are very numerous, and form more than one layer, are set close together, are evenly distributed over the fin, and occasionally may branch. In the adult fish, except near the distal growing edge of the fin, they are deeply embedded in the connective tissue some way from the epidermis (figs. 1 and 7 *ct.*), and overlap to a considerable extent the cartilaginous fin-supports. They are developed on both sides of the fin, and proximally embrace the median cartilaginous rays. The proximal ends of the *ceratotrichia* are enclosed in the sheet of connective tissue to which the special fin-muscles are attached (fig. 1, *cnt.*). These muscles, developed from the muscle-buds which sprout from the myotomes, are the appendicular muscles which occur in the fins of all fish, and are parallel to and correspond with the endo-skeletal rays. Outside the *ceratotrichia* and the surrounding layer of connective tissue lie the denticles, and lastly the epidermis. The denticles bear no relation either in position or in number to the underlying dermal rays.

Klaatsch (21) has given some details concerning the early development of the *ceratotrichia*. According to him cells derived from the epidermis migrate inwards into the underlying mesoblastic tissues, where they secrete the rays. The horny substance appears first in the centre of these “scleroblasts,” and subsequently enlarges and becomes surrounded by a multicellular sheath. These statements are supported by very unconvincing figures.

My own observations are directly opposed to Klaatsch's interpretation. Sections through embryos of *Scyllium* or *Acanthias* properly preserved, and treated with appropriate stains (such as borax-carmin and picro-nigrosin), show conclusively that a continuous and definite basement membrane separates the epidermis from the mesoblastic tissues over the whole surface of the animal (figs. 7—12 *b.m.*). At what stage this membrane first makes its appearance I am

unable to say ; but there can be no doubt that it is formed very early indeed. It is clearly present, for instance, in *Scyllium* embryos 14 mm. in length, long before either denticles or dermal rays have begun to develop. Once laid down the basement membrane remains, as far as can be seen, continuous and unbroken throughout embryonic life. Of any migration of scleroblasts from the epidermis there is not the slightest trace, and I have no hesitation in stating that it does not occur in the embryos I have examined.¹

After the deposition of the basement membrane, which stains dark blue with nigrosin, the actinotrichia begin to develop in those regions of the, at first, continuous median fin which are destined to give rise to the adult fins. Almost simultaneously ceratotrichia begin to develop in the paired fins. Since the fins grow at their free edge, the same section shows various stages in the development of the rays according as the parts nearer or farther from the body are examined. Near the edge itself the first origin of the rays can be traced.

Here the secreting cells are seen to lie close under the epidermis, and to deposit the horny substance, if not in actual continuity with, at all events in immediate contact with the basement membrane, on to the under surface of which they cling (figs. 8, 10, and 12). Thus the first rudiments of the dermal rays appear to be formed on the outer surface of the scleroblasts, which range themselves in parallel rows. Soon they seem to insinuate themselves between the ceratotrichia and the basement membrane, so that the ray becomes gradually separated off from the membrane as it grows older, and sinks farther and farther into the mesoblastic tissue (figs. 9, 11, and 7). In the meantime the young ray becomes surrounded by a sheath of secreting cells, and increases in bulk by the concentric addition of layer upon layer of fibrous horny substance. Occasionally the younger portion of the ray may be seen to be connected with the basement membrane by fine strands of cuticular substance, which, like the membrane and the ray itself, stains dark blue with nigrosin (fig. 9).

¹ Harrison (15) obtains the same results in Teleosts.

It is not till some time after the ceratotrichia have begun to develop that the overlying denticles make their appearance. In this paper it is not proposed to enter into a detailed description of the development of these structures; but I may point out that in its initial stages the denticle appears as a mere thickening of the basement membrane secreted by the mesoblast cells, which group themselves below its place of origin (figs. 11 and 7 *d*). The continuity of the denticle (the dentine cone) with the membrane is retained throughout its development.

By the time the denticles begin to develop, the ceratotrichia are separated from the epidermis by a considerable layer of fibrous connective tissue; and, moreover, since new rays are laid down at the growing edge of the fin, we may find several layers of ceratotrichia. As the fish grows older, the proximal thick ends of the ceratotrichia come to lie relatively closer to the median endo-skeletal fin-supports. Fig. 1 shows the relations of these structures in the adult.

Ceratotrichia occur in all living Elasmobranchs, although they may be much reduced in size and number in the highly specialised fins of the Rajidæ. So far as is known, no other kind of dermal ray whatever exists in these fish. The fossil Elasmobranchs, in this particular, seem to resemble in every essential their modern relatives.

Holocephali.

Chimæra and Callorhynchus are provided with dermal rays of exactly the same structure as those of the Elasmobranchs. The presence of typical ceratotrichia in the Holocephali confirms the view that this group is merely a highly specialised offshoot from the Elasmobranch stem.

Teleostei.

Passing now to the higher bony fish, we find quite a different state of things. The general structure and relations of the dermal rays of these forms are so well known that only a brief description is here necessary.

In the majority of Teleostean fish the median and paired fins are covered with a smooth scaleless skin, below which lie the dermal fin-rays. For reasons which will appear later, I propose to call these rays the lepidotrichia. They are, as a rule, both jointed and branched. Generally they are thicker and more rounded proximally, thinner and more flattened distally. The jointing is usually more conspicuous distally than near the base of the fin, where the divisions may be obliterated, this region of the ray frequently becoming rigid. By the more or less complete suppression of the branching and jointing, the lepidotrichia may in many cases become converted into the spines so often found in the fins of the more modified Teleosts.

The lepidotrichia, like the ceratotrichia, are present on each side of the fins. Since they correspond from side to side, fitting close together back to back, so to speak, they form apparently single, but really paired rays, capable of being split longitudinally into two. At the proximal extremity the two elements diverge and closely embrace the extremity of the median endo-skeletal fin-support. Here is generally situated a small distal endo-skeletal element, the so-called baseost, to which the dermal ray is firmly attached by ligament. These structures have been well described by Parker (29), Cole and Johnson (7), and Bridge (4). The various pterygial muscles (*m. erector*, *depressor*, *inclinator*), which are more elaborately differentiated than in the Elasmobranchs, spring from this proximal end of the fin-ray on either side of the baseost (Text-fig. 4, p. 488). Such are the typical structure and relations of the lepidotrichia in adult Teleostean fish. They are always present, and throughout the group they undergo no very essential change.

Whereas in the caudal and paired fins the lepidotrichia retain their primitive superiority in number over the endo-skeletal rays (see p. 486), in the dorsal and anal fins they correspond strictly to the latter in number and position. Each double dermal ray in these fins articulates with the extremity of one endo-skeletal fin-ray.

It is to be noticed that, as a rule, in the caudal fin of Teleosts (the morphological ventral caudal lobe) the proximal ends of the lepidotrichia are not, for the most part, attached to the extremities of the endo-skeletal supports; but have pointed, unjointed, terminal regions passing inwards on either side of the hypural bones or hæmal spines (figs. 59 and 25). The articulation of the lepidotrichia in the middle region of the caudal lobe is often more like that of the other fins, than near the edges. It will afterwards be seen that this peculiarity of the caudal lepidotrichia probably represents a more primitive condition retained and emphasised in relation to the stiff, unbending character of the caudal fin, which enables the Teleostean fish to swim so actively with its tail.

But there are two entirely different kinds of dermal rays in the fins of adult Teleostean fish. As was first pointed out by la Valette St. George, there are in the "adipose dorsal fin" of Salmonidæ and Siluridæ no lepidotrichia, but slender, unjointed, horny fin-rays essentially like the ceratotrichia of Elasmobranchs. Moreover at the distal free edge of all the fins of the Teleostei similar slender horny fin-rays are to be found (Lotz [24], Hertwig [17], Harrison [13]). It was long ago noticed by Agassiz (1) that the delicate median and paired fins of Teleostean embryos are supported by numerous fine, hair-like, dermal rays. Only at a comparatively late stage do the jointed lepidotrichia develop. Vogt (40), Lotz (24), Beaudelot (2), Hertwig (17), MacIntosh and Prince (25), Ryder (32), and Harrison (13) have since observed these rays both in the embryo and in the adult. To Ryder we owe the convenient name actinotrichia, which is now generally applied to them.

Lotz believes that the actinotrichia give rise to the lepidotrichia by coalescence and growth. Hertwig speaks of them as being involved in the formation of the adult ray, and Ryder adopts the same view. Harrison, who has lately, in an admirable paper (13), given a detailed account of the development of both kinds of dermal rays from their very first appearance in *Salmo*, shows that they are of inde-

pendent origin. My own observations on the development of the Teleostean dermal rays have also been chiefly made on young Salmonids, and confirm Harrison's results in most particulars.

The actinotrichia appear to develop just like the ceratotrichia of Elasmobranchs. They are visible at an early stage as fine threads, deposited by the secreting mesoblastic "scleroblasts" immediately below the basement membrane (fig. 20). This membrane is always present as a continuous layer staining dark blue with nigrosin in Teleosts, as in Elasmobranchs, and, indeed, in all the fish I have studied. Soon the scleroblasts push their way in between the ray and the membrane; and as they grow older and larger the actinotrichia get carried inwards farther from the epidermis (figs. 20 and 21). In quite young fish, where the lepidotrichia have scarcely developed, the actinotrichia bear much the same relation to the connective tissue and the endoskeleton, as do the ceratotrichia in Elasmobranchs. They become surrounded by the secreting cells, and grow in thickness by the addition of concentric layers of substance. In the adipose fin (especially of Siluroids) they may reach quite a considerable size, and may branch distally. But in the other fins, where lepidotrichia are formed, the actinotrichia do not increase much in length. Either they get re-absorbed proximally as fast as they are secreted distally, or they get bodily carried outwards in the growing edge of the fin. In the adult Teleostei the actinotrichia are relatively very small, and rarely extend along more than one or two joints of the overlying lepidotrichia. Excepting in the adipose fin, where they form an evenly distributed layer over the web as in Elasmobranchs, the actinotrichia become grouped together more closely in the region where the lepidotrichia develop, and gradually thin out in the intervening spaces. An adult jointed fin-ray thus acquires the deceptive appearance of being frayed out into fine threads at its outer extremity.

Some considerable time after the actinotrichia have been formed, the definitive dermal rays, or lepidotrichia, put in

an appearance. Beaudelot (2), Hertwig (17), Ryder (32), and especially Harrison (13), have given such complete accounts of their development that there remains little to discuss beyond their relation to the basement membrane, and the mode of origin of the articulations.

The lepidotrichia are first seen in transverse section as thickenings of the basement membrane laid down over an area of considerable width by the underlying mesoblastic scleroblasts (figs. 24, 20, and 21). At this early stage in the development of the ray, the thickening is directly continuous with the membrane extending in unbroken line between adjacent lepidotrichia. As the thickening becomes more pronounced, it begins to bend with its convexity outwards, and the edges become more and more sharply marked off from the ordinary basement membrane. The scleroblasts now begin to insinuate themselves round the edge of the growing lepidotrich as it becomes, so to speak, peeled off from the membrane (fig. 22). During the whole process of the separation of the dermal ray from the basement membrane, the latter is never broken. New cuticular substance is deposited as fast as the mesoblastic cells grow round on to the outer surface of the ray. For a long time, perhaps throughout life, strands of cuticular substance extend from the basement membrane to the lepidotrichia, which never sink very far from the epidermis, except quite at their proximal ends (fig. 23).

The young lepidotrichia are flattened in section, and grow chiefly by the addition of new layers of bony substance on their outer and inner surfaces. At first, as is generally the case with Teleostean bones, we find only a thin layer enclosing no bone-cells; but as the ray grows older and thicker, cells become included, and it acquires the normal structure of Teleostean bone.

The branching of the lepidotrichia is not due to the proximal fusion of originally distinct rays, as Hertwig states (17), but, on the contrary, to the repeated subdivision of the growing distal end of an originally single ray. That this is the case in

the Teleostei becomes obvious when we consider that from their first appearance the lepidotrichia in the anal and dorsal fins correspond in number with the bascosts. The branching of all dermal rays is most probably brought about in the same way. As in the Elasmobranch, so in the Teleost, the various stages in the development of the dermal rays can be seen in passing from the free edge towards the base of the fin. In the Teleost, however, a second generation of lepidotrichia is never produced.

It will be understood from the above description that the lepidotrichia succeed the actinotrichia, and are developed outside the latter; so that a section taken through the growing edge of a fin, where both structures are present, invariably shows the actinotrichia occupying the more internal region, and the lepidotrichia between them and the epidermis.

Harrison states that in *Salmo* the articulations of the lepidotrichia are secondarily formed by the breaking through of proliferating osteoblasts, which subsequently mould the joint (13). This rupture of an originally continuous bony lamina would occur very early in the development of the ray at its growing end, where it is still quite thin. I venture to think that this interpretation is not correct. My own observations lead me to the conclusion that whilst, on the one hand, the dermal ray may be said to be almost continuous—the articulation being bridged over by softer, more elastic, and non-calcified tissue,—yet, on the other hand, the joints are marked out as soon as the ray becomes separated off from the basement membrane. There appears to be no breaking of an originally continuous hard piece; the osteoblasts migrate to the outer side rather round than through the ray, and the articulation becomes suddenly conspicuous owing to the deposition of new outer layers of bony matter on each side of the joint. At all events, I can affirm that joints appear at a distance from the edge of the fin which is less than the length of a complete segment of the dermal ray.

It is clear that although the actinotrichia precede the definitive rays, and although they may occasionally become

included in the bony substance forming the lepidotrichia, yet they cannot be said to give rise to the latter by coalescence or growth.¹ In fact, the actinotrichia take no important part in the formation of the lepidotrichia, and the two kinds of dermal rays are of distinct origin. The general relations of these structures in the Teleostei are illustrated in Text-fig. 4, p. 488.

There are many Teleostean fish in which the scaling of the body spreads over the opercular region and the skull, to a greater or less extent. That this extension of the scales over bones of dermal origin is secondary can scarcely be doubted. The same tendency for the scales to spread may be observed on the fins, especially the caudal fin, of many Teleosteans (fig. 59). It is carried to an extreme in such cases as *Chaetodon* and *Hæmulon*,² where all the fins are covered with minute scales similar in character to those of the body. These small scales lie on the outside of the lepidotrichia, which are normally developed, and to which they bear no direct relation in number or in disposition (figs. 66 and 67). The significance of these facts will be further discussed later on (p. 491).

Amia.

In *Amia calva* the jointed dermal rays resemble the lepidotrichia of the Teleostei in every particular, both with regard to their structure and development, and with regard to their relation to the endo-skeletal fin-supports. Actinotrichia are also found in the young, and at the edge of all the fins in the adult.

Lepidosteus.

The "bony pike" is provided with lepidotrichia and actinotrichia in every essential like those of the Teleostei. But it

¹ I have confirmed this statement on several genera, amongst others on *Chaetostomus*, a Siluroid closely allied to those studied by Hertwig.

² I am much indebted to Mr. G. A. Boulenger for the gift of specimens of *Chaetodon* and *Hæmulon*, and also for many useful suggestions.

is important to notice that, in their histological characters, the segments of the lepidotrichia closely resemble the body-scales, as has often been mentioned by previous writers. The scales, like the segments of the dermal ray, are joined together by ligamentous connective tissue. A transverse section through both scale and ray exhibits the same bony and ganoine layers.

A study of the development of the dermal rays of *Lepidosteus* shows, firstly, that the actinotrichia are peculiarly well developed at the edge of the fins (fig. 19), where they are thicker, longer, and more extensively distributed than in most Teleosts; secondly, that the segments of the definitive ray develop in exactly the same way as do the lepidotrichia of *Salmo*. They appear first as thickenings of the basement membrane, which become separated off, and rapidly grow in thickness as they sink inwards. Soon they acquire bone-cells and Haversian canals, and lastly a covering of ganoine is deposited on the outer surface. The structure and development of the body-scales of *Lepidosteus* have been studied of late years by Hertwig (17) and Nickerson (26); and it has been shown that a number of small denticles of often transient nature are developed on the outer surface of the scale. Quite similar denticles are also found on the young segments of growing lepidotrichia. Text-fig. 2, p. 485, illustrates the relations of the dermal skeleton of the fins of *Lepidosteus*.

Polypterus.

The general structure and relations of the jointed dermal rays of this interesting fish have already been described by Hertwig (17), Bridge (4), and Boulenger (3). Although highly specialised in some respects, they conform on the whole to the ordinary Teleostean type of lepidotrichia. The anal fin is remarkable in that the dermal rays have preserved the more simple and primitive relation to the endo-skeletal supports. The lepidotrichia here have pointed terminal segments

which pass inwards below the body-scales, as in the caudal fin, and are not related to a particular baseost element, as in the higher fish described above. The lepidotrichia of the ventral caudal lobe bear the same relation to the endoskeleton. In their histological structure the dermal rays closely resemble those of *Lepidosteus*.

On examining sections through the growing edge of the fins, we find very well developed actinotrichia (fig. 17). The lepidotrichia arise, as usual, as a thickening of the basement membrane. As they grow older the segments gradually acquire a structure exactly similar to that of the body-scales, with a covering coat of ganoine (figs. 60 and 61). Moreover the young rays are provided on their outer surface with a number of small denticles (figs. 18 and 60) like those found in *Lepidosteus* and *Hypostoma*. There can be no possible doubt that the actinotrichia and lepidotrichia of *Polypterus* are strictly homologous with the actinotrichia and lepidotrichia of the "*Actinopterygii*" (*Teleostei* and *Ganoidei*).

Acipenser.

Hertwig (17) has already described the dermal rays of the *Acipenseroids*. In adult sturgeons the actinotrichia are very well developed at the edge of the fins. The lepidotrichia, originating just as in the *Teleostei* and "*bony Ganoids*," soon acquire a bony structure like that of the body-plates and scales, and also small bony spines, which are considered by Hertwig to represent degenerate denticles.

In the *Acipenseroids*, or *Chondrostei*, the lepidotrichia are much more numerous than the endo-skeletal fin-rays. Their proximal ends overlap the cartilages, especially in the impaired fins, more than is the case in the higher fish; and they are not so closely connected with the endo-skeleton. In fact, the general relations of the lepidotrichia to the endoskeleton and muscles somewhat resemble those of the ceratotrichia in *Elasmobranchs*. They are shown in fig. 2, and Text-fig. 3, p. 487.

Dipnoi.

Ceratodus seems to be the only Dipnoan of which the dermal rays have been described in any detail. Günther (12), in his well-known memoir on the Australian lung-fish, gives the following account of the dermal rays, which he calls the "dermo-neurals" and "dermo-hæmals":—"They are exceedingly numerous, four or five or more corresponding to a single vertebral segment, and form a double series, one series on each side of the fin. This peculiarity, which *Ceratodus* has in common with *Lepidosiren*, reminds us of those fin-rays of Teleosteous fishes which can be more or less completely split into a right and left half. The dermo-neurals of *Ceratodus* are not articulated to the extremities of the inter-neurals, but overlap them for a considerable distance of their length. . . . No ossification takes place in either of them; they consist entirely of cartilage in which numerous spindle-shaped cells are embedded, many of these cells being produced at both ends into a very long process." Günther evidently considered the dermal rays of *Ceratodus* to be simple, unjointed, and unbranched, since he contrasts them with the jointed and branched rays of *Dipterus*.

The structure of the dermal rays of the Dipnoi is so important from the point of view of classification that it is necessary to discuss the subject in detail.

In the adult *Ceratodus* the median fins pass gradually into the body; there is no sharp line of demarcation between the two. The body-scales extend evenly on to the fin, where they become smaller, more numerous, and of a more elongated shape (fig. 3). The more distal scales become ranged in rows parallel with the underlying dermal rays, but not strictly corresponding to them. The scales do not reach the actual margin of the fins, ceasing some little way short of it.

These scales are, of course, covered by the epidermis, and lie embedded in the connective tissue where they are formed. Below the scales, and therefore in the still deeper layers of

the connective tissue, are found the dermal rays. They are in the form of slender pliable rods, about five times as numerous as the endo-skeletal fin-supports, which they overlap (fig. 3, *kpt.*). The proximal half of the ray is stouter and more cylindrical than the more distal region, which becomes flattened and thinned out peripherally to a mere thread. This proximal region is also harder, owing to more complete calcification, and is never jointed. Some of the dermal rays appear to remain unbranched and unjointed throughout life, but most of them become both branched and jointed in the distal region (figs. 3, 36, 37).

The joints occur in the most irregular manner, beginning either near the middle of the ray, or near its tip; sometimes they are numerous and close together, and at other times few and far between. The pointed inner ends of the majority of the dermal rays reach proximally to an even level in the sheet of connective tissue surrounding them; the fin-muscles are attached to this connective tissue and to the dermal rays themselves. The region where the joints first appear at the distal end of the unjointed piece may be considered as roughly indicating the limit where the body ends and the fin begins.

This description applies almost equally well to the paired fins, where, however, the rays are shorter and more frequently jointed (fig. 37).

The dermal rays of *Ceratodus* are formed of fibrous substance of horny consistency, which becomes calcified and hard in the older regions. Here also the included cells become very numerous, and in favourable preparations can be seen to be provided with a multitude of fine branches (fig. 41). The older and thicker parts of the ray acquire the structure, not of cartilage, as stated by Günther, but of fibrous bone. It is to be noticed that the substance of the ray becomes subdivided into an inner and more fibrous region, and an outer thinner layer, which appears more refringent and is more thoroughly calcified (figs. 29, 34). This outer layer alone is sharply interrupted at the articulations. The proximal un-

jointed region is formed chiefly of the harder outer layer; the distal region, on the contrary, chiefly of the softer inner layer.

Protopterus is provided with dermal rays of essentially the same structure. They differ, however, in being smaller, softer, less calcified, less frequently jointed and branched, and in having fewer cells included in their substance.

In *Lepidosiren*, again, the dermal rays, although of the same nature, are still further reduced. They have disappeared altogether from the paired fins, and in the unpaired fins are shorter, very soft, scarcely jointed, and unbranched.

Protopterus is the only Dipnoan in which I have been able to study the development of the dermal fin-rays.¹ Sections through the median fins show the usual basement membrane separating the epidermis from the underlying mesoblastic tissues. Towards the growing edge of the fin, immediately below the basement membrane, can be seen the early stages in the development of the ray, in the form of a delicate thread of cuticular substance secreted by rows of scleroblasts (figs. 13 and 14). The distal extremity of the thread does not appear to originate distinctly as a mere thickening of the membrane, but becomes smaller and smaller on passing outwards, and finally becomes indistinguishable from a network of connective-tissue fibres underlying the basement membrane. As it grows, the ray sinks away from the membrane and becomes surrounded by the secreting scleroblasts. Very soon the distinction between the outer and inner regions can be made out (figs. 15 and 16). A fairly definite sheet of connective tissue joins the dermal rays together, some distance below the epidermis (fig. 16). Meantime the scales develop on the body and spread over the proximal region of the fin; on the outer surface of the rays.

Neither in adult Dipnoi, nor in the larva of *Protopterus*, have I found any trace of actinotrichia. It is possible that

¹ Mr. J. S. Budgett very kindly presented me with two larvæ of *Protopterus*, on which these observations have been made.

they are present in the quite young stages of development ; but they are not figured by Semon (33).

THE STRUCTURE AND HOMOLOGIES OF THE DERMAL RAYS OF LIVING FISH.

We may now briefly recapitulate what has been said above concerning the dermal rays of living fish, and discuss their homologies.

There are four different kinds of dermal rays, or dermatrichia, in adult living fish :

1. The horny rays, or ceratotrichia, of Elasmobranchii and Holocephali : fibrous, flexible, unjointed, rarely branched, cylindrical rods. Like all dermal rays, they are developed on both sides of the fin-folds both of the median and of the paired fins. The pointed proximal ends overlap on each side the median endo-skeletal fin-supports, and the tapering growing distal ends reach the free edge of the fin. Ceratotrichia are of the same structure throughout, grow by the addition of concentric layers of substance, and never contain any bone-cells. They originate as fibrils secreted by mesoblastic scleroblasts in contact with the inner surface of the basement membrane. As they grow older they sink inwards, new layers of connective tissue being formed outside them. During the growth of the fin new generations of ceratotrichia may be added, so that a section of a fully grown fish may show a layer of rays several deep on either side. The bony denticles of the skin lie outside, and are quite independent of the underlying rays, which are the first to make their appearance in the embryo (Text-fig. 1).

2. The actinotrichia : delicate little "horny," unjointed, and usually unbranched rays found in the fins of all living Teleostomes as the first, and for some time the only, rays in embryonic or larval life. In later stages they become functionally replaced by the bony rays, except in the adipose fin. The actinotrichia, however, persist throughout life near the free growing edge of all the fins. They develop like the ceratotrichia, and appear to be in every respect similar to

them.¹ The actinotrichia are more numerous than the jointed rays which develop outside them, and become grouped together at the edge of the fins below the growing definitive rays (Text-figs. 2—4).

3. The definitive bony fin-rays, or lepidotrichia: typically ossified, jointed, and branched. These dermal rays

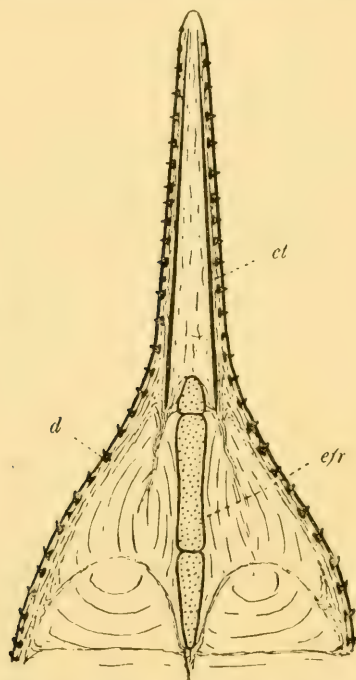


FIG. 1.—Diagrammatic figure of a section through the dorsal fin of *Scyllium*. For the lettering see p. 517.

are found in all Teleostomes, in both the paired and unpaired fins (excepting the "adipose" fin). The hard ossified segments are joined together by narrow, fibrous, uncalcified regions, forming flexible articulations, comparable to the ligaments uniting ganoid scales to each other. In specialised forms the lepidotrichia may undergo various modifications,

¹ Should this conclusion be borne out, the name actinotrichia might perhaps be dropped in favour of the more descriptive term ceratotrichia.

and are often converted into spines by the suppression of the joints.

The development of the lepidotrichia is somewhat different from that of the ceratotrichia. They appear as thickenings of the basement membrane of considerable width, secreted by

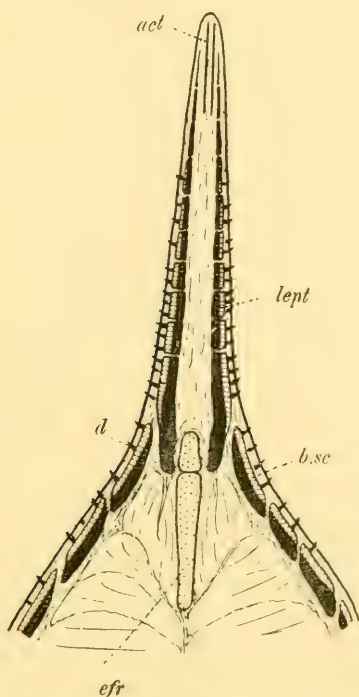


FIG. 2.—Diagrammatic figure through the dorsal fin of *Lepidosteus*.
For the lettering see p. 517.

underlying scleroblasts. Later they become separated off from the membrane as thin plates of bony substance, which sink inwards and become surrounded by the mesoblastic tissues. In forms like *Polypterus* and *Lepidosteus*, with ganoid scales, the segments of the dermal rays acquire the same histological structure as the body-scales; they have the same covering of ganoine and the same minute denticles on

their surface. Hertwig long ago showed that this is also the case in Siluroids and Acipenseroids, where the segments of the lepidotrichia resemble in every detail the spiny plates and scales on the body. As we pass to the more highly specialised Teleosts, with cycloid and ctenoid scales, the resemblance between the segments of the rays and the body-scales becomes less obvious, the lepidotrichia preserving, as a rule, a more primitive and truly bony structure. But in the highest Teleosts both the endoskeleton and the lepidotrichia may lose the bone-cells.

Whilst in the lowest Teleostomes, like Acipenser, the lepidotrichia are much more numerous than the endo-skeletal rays, overlap the latter to a considerable extent, and are not specially differentiated at their proximal ends; in the "bony Ganoids" and the "Teleostei" they come to correspond strictly in number with the endo-skeletal supports, to the small distal element of which (the "baseost") they become closely connected. The proximal segment of the lepidotrichia in these fish becomes enlarged and differentiated for clasping the baseost and for the attachment of muscles. This modification is carried out more completely in the higher than in the lower forms (Polypterus), and more completely also in some fins than in others (Text-fig. 4).

4. The dermal rays of the living Dipnoi, or camptotrichia, may be considered, for present purposes, as a fourth and distinct variety of ray, somewhat intermediate in character between the ceratotrichia and the lepidotrichia. Like the former, they are much more numerous than the endo-skeletal fin-supports, and overlap them on either side. In Ceratodus, where the dermal rays are best developed, they are seen to consist of a slender rod of fibrous, flexible material, which acquires the appearance and consistency of fibrous bone in its older and thicker parts. A large number of branching cells are distributed throughout the substance of the ray, which may be distinguished into an inner and an outer more calcified region. The camptotrichia may branch, and are generally jointed. As a rule they are subdivided into a more

cylindrical, unjointed proximal half, and a flatter, irregularly jointed distal half in the fin itself. The proximal ends bear much the same relations to the muscles as do the lepidotrichia. The body-scales extend over the dermal rays to near the edge of the fins. These camptotrichia are deeply embedded,

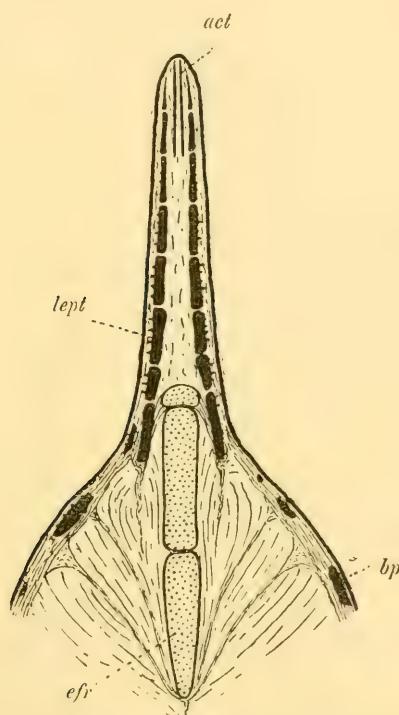


FIG. 3.—Diagrammatic figure of a section through the dorsal fin of *Acipenser*. For the lettering see p. 517.

whereas the scales are in the more superficial layers of connective tissue (Text-fig. 5).

Such is the structure of the dermal rays in living fish, and the relations of these rays to the scales, the muscles, and the endo-skeleton are illustrated in figures 1, 2, 3, and 59, and in the text-figures. We now endeavour to trace out their origin and homologies.

Ryder (32), the only author who seems freely to have speculated on this subject, believed all the dermal rays to be homologous with and derived from the "horny" type found in Elasmobranchs. Concerning the origin of these ceratotrichia little can be said. That they should have been

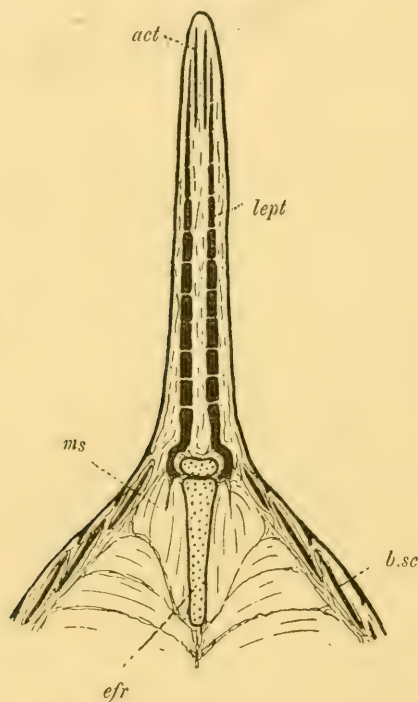


FIG. 4.—Diagrammatic figure of a section through the dorsal fin of a Teleostean fish. For the lettering see p. 517.

derived from the basal plates of the denticles, as suggested by Klaatsch (21), if I understand him rightly, seems most unlikely. Neither in their development nor in their structure have the two anything in common, beyond the fact that they are both produced in the mesoblast. The rays develop in the fins long before the denticles themselves put in an appearance.

With regard to the actinotrichia, their universal presence in all the widely diverging groups of Teleostomes suggests that they are of very ancient origin. Most writers, like Beaudelot (2), Ryder (32), Harrison (13), compare them to the ceratotrichia. As Beaudelot says, "Les nageoires des

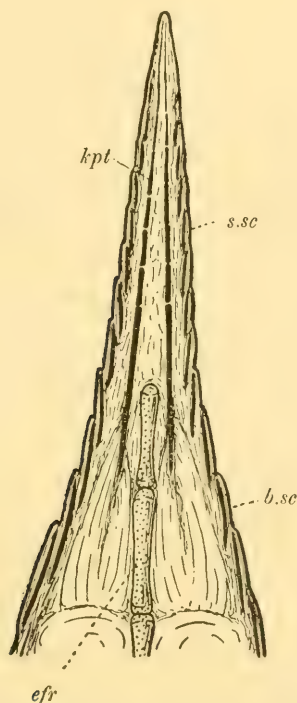


FIG. 5.—Diagrammatic section through the dorsal fin of *Ceratodus*.
For lettering see p. 517.

premiers [Selachians] avec leur filaments cornés pour squelette, correspondant évidemment à la nageoire embryonnaire des seconds [Teleosteans],” with its “filaments cornés.” There can be little doubt that these two kinds of rays are homologous. Of similar shape, structure, and developmental history, they must surely be of common origin. In adult living Teleostomes, however, they would appear to be only

vestigial organs of little mechanical importance, having been functionally superseded by the bony rays.

To what origin are we to trace the lepidotrichia which appear in the Teleostomes? They may be organs *sui generis*, developed in these fish only; or they may be derived from the ceratotrichia of Elasmobranchs, as held by Ryder; or, again, they may be homologous with the body-scales. The evidence seems to be strongly against the first of these views. With regard to the second, it should be remembered that the ceratotrichia in their development and structure exhibit constant and important differences when compared with the lepidotrichia; and that, as we pass from the higher to the lower Teleostomes, we can trace no distinct approximation in character of the Teleostome type of ray to the Elasmobranch type.

The third view is the one held by Beaudelot (2)¹, Gegenbaur (11), Hertwig (17), and others. Strong evidence in favour of this theory, that the dermal rays of the Teleostomes are of the same nature as the body-scales, is afforded by their histological structure and their development. This is especially the case in forms which exhibit a more primitive dermal skeleton; as, for instance, in *Lepidosteus*, *Polypterus*, and *Hypostoma*,² where, as we have seen, the parallelism in structure is complete, down to the possession of more or less transient denticles on the outer surface.

It is true that in the higher Teleostean fish, with thin lamellated scales, the divergence between the two sets of organs is very considerable; but this may be traced to the fact that, whilst the body-scales have become extremely

¹ "Établir l'identité de structure des rayons natatoires et des écailles, c'est établir la parenté de ces deux ordres de productions."

² Hertwig writes: "Bei *Hypostoma* und *Callichthys* besitzen die verschiedenen Theile des Hautskelets, die Tafeln und Schilder des Rumpfes, die Plättchen und Stacheln des secundären Flossenskelets, die belegknochen des primären Schultergürtels und des Primordialeranium einen gemeinsamen Ursprung, indem sie phylogenetisch durch Verschmelzung gleichartigen in den oberflächlichen cutislamellen dicht bei einander liegender kleinster Knochenplättchen, die je ein Zähnchen tragen, entstanden sind" (17).

specialised in structure, the dermal rays may have preserved many primitive characters which the scales have lost. Into the question of the exact homology of the Teleostean scale itself I do not propose to enter; we may well adopt the generally accepted view that they were derived originally from the bony basal plate of the "placoid" scale. It should also be borne in mind that it might be urged that the thin scales of modern Teleosts may possibly represent a second generation of dermal organs, substituted for and developed outside the older scales. The familiar fact that the scales in these fish may overlie the dermal bones of the skull and opercular apparatus, and may cover the lepidotrichia themselves (as in *Chaetodontidæ*, see page 477), seems to support this theory. For my own part, however, I am inclined to believe that such an interpretation is both unjustified and unnecessary, and that the overgrowth mentioned above is merely due to the late and secondary extension of the scaling of the body. Even in the sturgeon itself we can see small bony plates occasionally overlying the bases of the dermal rays.

Hitherto I have omitted to mention the "fulcral" scales found at the edge of the fins of *Acipenseridæ* and *Lepidosteus*. In *Acipenser* these fulcra consist of V-shaped scales situated along the dorsal surface of the caudal lobe. They obviously belong to the same category of dermal skeletal organs as the scales, and probably represent a right and a left scale fused together. In *Lepidosteus* fulcral scales occur along the anterior edge of the dorsal, anal, and paired fins, and along both the dorsal and the ventral edge of the caudal fin. But in this fish the fulcral scales are in double rows, not fused together. Now whilst the fulcra pass insensibly into the body-scales, as was long ago pointed out by Agassiz (1), and are undoubtedly modified scales, their resemblance to the neighbouring lepidotrichia points to the same conclusion with regard to the latter. As Burckhardt remarks, "Fulcra, Flossenstrahlen und Schuppen sind zweifellos verwandte Hartgebilde" (6).

It will be seen below, when we come to discuss the structure of the extinct forms, that the evidence is overwhelmingly strong in favour of the theory that the jointed dermal rays or lepidotrichia, of at all events the lower Teleostomes, are in a general sense homologous with the scales of the body. But it will also appear that the problem is really not as simple as it would seem to be at first sight, and that, from what we know of the dermal rays of the Dipnoi, there is some reason to believe that the lepidotrichia may after all be structures of compound origin, formed by the fusion of ceratotrichia with overlying scales (p. 498).

The dermal rays of the Dipnoi combine certain of the characters of both the ceratotrichia and the lepidotrichia. Whilst they resemble the former in their fibrous and flexible structure, their more or less rounded shape, their deeply inserted proximal ends overlapping the endo-skeleton, and their early development, they are like the lepidotrichia in their possession of bone-cells, of calcification, of joints, and in their situation below the body scales. To decide to which category they belong seems almost impossible from the evidence afforded by the few surviving genera so imperfectly known. The apparent absence of actinotrichia is another difficulty in the solution of this problem, the discussion of which we will defer until the extinct Dipnoi have been dealt with.

THE DERMAL RAYS OF FOSSIL FISH.

The dermal fin-rays of the extinct Elasmobranchs, as has already been mentioned above, differ so little from those of their modern representatives that they need no further description. In *Cladoselache*, ceratotrichia have been described and figured by Dean (8); but I have not been able to find them in the paired fins.

Ceratotrichia quite similar to those of the Elasmobranch fish are found in the pectoral fins of Acanthodians. They have been described in detail by Reis (31). Rows of small

scales similar to those on the body cover the caudal fin; transverse sections might possibly reveal underlying ceratotrichia.

Amongst the Ichthyotomi, *Xenacanthus* is the only genus in which dermal rays have been described. They appear to be typical ceratotrichia, differing only from those of Selachians in that they were perhaps grouped together near the endoskeletal rays in the paired fins (Fritsch [10]).

No very definite dermal rays have been described in the Ostracodermi. Most authors seem to agree that these aberrant fish had median fins provided with rows of small scales resembling those on the body in histological structure. Writing of the *Asterolepidæ*, Traquair says, "No distinct 'rays' can be seen" (37). In his recent description of *Birkenia elegans*, the same author describes the caudal fin thus:—"Along the dorsal margin we have a special band of tiny, narrow, oblique scales, which would remind us of the ridge-scales or 'fulcræ' of the upper lobe of a palæoniscid tail, were it not that the band here apparently consists of two rows of scales one above the other. The fin-membrane is also covered with narrow scales, which tend to be arranged linearly so as to give the fin a very decidedly rayed appearance. All the scales of the tail and of the caudal fin show the same minutely tuberculated ornamentation which occurs on the scutes of the body" (38). A. Smith Woodward, describing *Cephalaspis Murchisoni*, Eg., says, "There are no well-defined fin-rays, the supporting structures being small, oblong, calcified plates, closely fitted together, and placed end to end in vertical parallel series" (42). My own observations on the *Cephalaspidæ*, especially on a specimen in the Oxford Museum, lead me to the conclusion that the fin-rays of *Cephalaspis*, at all events, were well-defined and typical lepidotrichia as regards their shape and disposition. The limits of the individual segments in this specimen are indistinct; but they are set end to end to form definite parallel rays of considerable width, and set very close together,—very much as in *Acipenser*, for instance. The presence of a very

extensive bony skeleton, of scales and plates on the body, of lepidotrichia and occasionally of fulcra on the fins, and of a heterocercal tail, seems to support the old-fashioned view that the forms included in the group Ostracodermi are really very specialised offshoots from the Teleostome stem. A detailed microscopic examination of their fins is urgently needed.

The fins of *Coccosteus* seem to have been devoid of dermal rays.

We may now leave these imperfectly known and very aberrant groups of fish, and pass directly to the consideration of the Teleostomes.

Although the various orders of fossil Teleostomi differ from each other in certain details of the structure of their dermal rays, yet they all possess unmistakable lepidotrichia of very uniform character. Only with respect to the proximal end do the dermal rays exhibit any considerable divergence of form. It will be most convenient to begin with those extinct fish which are most nearly related to the surviving groups of Teleostei, and to work back to the more primitive forms. For this purpose we shall adopt the classification set forth by A. Smith Woodward in his excellent British Museum catalogues, and in his text-book (42 and 43).

Actinopterygii.

Isospondyli.—Amongst the great variety of fish included in this group (the Teleostei and their earlier extinct relatives) it is not until we reach the Leptolepidæ that any important change in the structure of the dermal rays can be observed. In this family ganoine first appears on the surface of the rays and scales. Not only have the Oligopleuridæ and Pholidophoridæ a covering of ganoine on the lepidotrichia and body-scales, but rows of typical fulcral scales are present at the edge of their fins. Fig. 62 shows the lepidotrichia of *Pholidophorus* in transverse section, and figs. 63 and 64 are drawn to illustrate the remarkable parallelism in histological structure which occurs between the scale and the ray. The

bone-cells of the lepidotrichia are seen to be of just the same type as those of the scale, if somewhat smaller.

Protospondyli.—The extinct fish allied to *Amia* give evidence of having had quite the same history. On passing from the more modern to the earlier and more primitive types, such as the *Semionotidæ*, *Macrosemiidæ*, and *Eugnathidæ*, we recognise the appearance of ganoine on the surface of the lepidotrichia, and of fulcral scales at the edge of the fins. There is also an increasing correspondence between the body-scale and the ray in histological structure.

Ætheospondyli.—The same story is told by the remains of these fish, with this difference,—that even the living *Lepidosteus* has lost neither the ganoine nor the fulcræ (p. 477).

Chondrostei.—We now come to a group of fish whose dermal rays are of a distinctly more primitive character than are those of the foregoing sub-orders of the *Actinopterygii*. In all the known *Isospondyli*, *Protospondyli*, and *Ætheospondyli*, the lepidotrichia correspond in number with, and are articulated to, the endo-skeletal supports in the dorsal and anal fins. Moreover these rays scarcely penetrate below the body-scales, except where a secondary overgrowth of the scale-bearing skin has taken place. In the *Chondrostei*, on the contrary, the dermal rays are always more numerous than the endo-skeletal supports, and are not specially related to the latter, but form an evenly distributed layer over the fin (see p. 479). The proximal segment of the lepidotrichia extends some little way beneath the body-scales, so as to embrace and overlap the extremity of the endo-skeletal ray.

In the degenerating series which leads from the *Chondrosteidæ* to the *Acipenseridæ* (A. S. Woodward [42]), we can trace the same tendency to lose the ganoine and the fulcral scales so constantly met with in those groups of fish which have survived to the present day. But in the other families of the *Chondrostei* these characters are generally well preserved. The *Palæoniscidæ* are by far the most instructive family to study for our present purpose. The

general structure of the lepidotrichia has already been well described by many authors, among whom one may mention especially Agassiz and Traquair in their admirable monographs (1 and 36).

The lepidotrichia of *Palæoniscus* do not differ much in their general relations from those of *Acipenser*. On examining a tail of a *Palæoniscid* we are at once struck with the strong resemblance the flattened shiny segments of the rays bear to the scales on the caudal region of the body. Yet even here the transition from the one to the other is not perfect, and may even be abrupt (figs. 52, 53). In the allied genus *Amblypterus*, however, as was pointed out to me by Dr. Traquair, the transition is so gradual that it is scarcely possible to say where the scales end and the rays begin (fig. 55 A and B).

An examination of this fish must, I think, dispose of all doubt as to the general homology of the two sets of structures. It need hardly be added that in the *Palæoniscidæ* the agreement in the details of histological structure between the lepidotrichia and the scales is as close as in their outward appearance.

Agassiz believed that, in some species at least, the fins were covered with scales, overlying the true dermal rays—"dans les *Palæoniscus Blainvillei* et *Voltzii*, du moins, il est évident que les divisions transverses que l'on voit sur les nageoires proviennent des séries d'écailles qui en recouvrent les rayons, et qui même sont placées de manière à reposer sur les bords avoisinans de deux rayons, . . . car en enlevant soigneusement ces petites plaques, on voit en dessous celles du côté opposé alterner avec l'empreinte des rayons" (1). But Traquair has shown that this view is not correct, and that no other separate set of rays underlies the scale-like lepidotrichia—a conclusion which is confirmed by my own observations.

It is to be noticed that in *Palæoniscus* the proximal segment of each ray is considerably longer than the others, and passes beneath neighbouring body-scales for some distance.

This buried portion of the ray may be compared to the bevelled part of a scale, which is covered over by the next scale in front, and both are devoid of ganoine (fig. 53).

We must now study the interesting and aberrant genus *Cheirolepis*, which, it will be remembered, is the oldest known representative of the group. *Cheirolepis* is remarkable for the possession of a covering of very minute scales, so small that the skin resembles rather the shagreen of a shark than the ordinary scaling of a fossil "Ganoid." Yet, judging by their microscopic structure, these dermal ossifications are not denticles, but merely ganoid scales of unusually small size (figs. 47 and 49). The fins are provided with the familiar fulcral scales at their front edge, and are supported by lepidotrichia, the segments of which are very numerous and minute. The segments of these rays are, in fact, of just the same size and appearance as the neighbouring body-scales, and, like them, are covered with a thick layer of ganoine, and ornamented with the same superficial sculpturing (figs. 47 and 49). Sections through the body-scales show that they are provided with a rather shallow base of bony substance containing bone-cells. Similar sections through the lepidotrichia, taken near the body, show that the segments have a much more extensive bony base of identical histological structure, but of much greater bulk and of more rounded shape (figs. 46 and 48). Towards the periphery of the fin the rays become flatter. At their proximal ends the lepidotrichia are continued beneath the body-scales in the form of unjointed bony rods, some six or seven times the length of a single outer segment. These unjointed pieces are seen to be of oval section, without ganoine, and of exactly the same nature as the inner part of the more distal region of the dermal ray, of which they form, so to speak, the continuation. The overlying ganoid scales are arranged in regular rows, closely fitting the rays, and perhaps really alternating with them, as seems to be suggested by the section figured (fig. 47). But the exact relative position of these superficial scales is very difficult to determine in the fossils

at my disposal. Some appearances have led me to believe that they are fused together in parallel rows along the top of the long proximal segment of the dermal rays. At all events they are set very close together (fig. 49 A). It was, perhaps, such an arrangement as I have just described in *Cheirolepis* which led Agassiz to believe that the fins are provided with dermal rays lying below more superficial scales. It must be remembered, however, that the elongated proximal segment of the lepidotrichia is situated, not in the fin, but in the body itself, and probably overlapped the endo-skeleton. Pander (28) fully adopts the view of Agassiz when describing *Cheirolepis*. From his figures and statements there can be no doubt that he fell into the mistake mentioned above. Traquair, on the contrary, considers that the rays consist of one layer of small segments only (35). The interpretations of these two authors can, however, be reconciled if we assume that Pander examined the proximal end of the rays, and Traquair the more distal region in the fin itself.

On comparing *Cheirolepis* with *Palæoniscus* the simplest conclusion would be that the proximal elongated joint buried beneath the scales in the former, is homologous with the proximal but only partially covered joint of the ray in the latter. If this basal joint, which in *Palæoniscus* is still covered with ganoine at its outer exposed end, were to become longer and to sink deeper beneath the body-scales, we should obtain the structure found in *Cheirolepis*. The proximal joint of the *Cheirolepis* ray is rounded in section, and exhibits unmistakable signs of concentric layers of growth (fig. 47), a fact which raises some doubt as to its original derivation from a superficial scale; but there is a general tendency, so to speak, for the deeper ends of the lepidotrichia to acquire this concentric structure, which is visible to some extent in the more distal segments themselves and in the scales (figs. 46 and 47).

Another interpretation is, indeed, possible—namely, that these dermal rays are compound structures formed by the fusion in the fin region of deep rays, homologous with the

ceratotrichia of Elasmobranchs, with overlying genuine scales, and that the two elements remain separate beyond the base of the fin, where they enter the body. This view will be further discussed below (p. 510).

To conclude, it may be said that the evidence derived from the study of the fossil Actinopterygii points undoubtedly to the view that the lepidotrichia are homologous with the body-scales, from which they have been partially, if not entirely derived. Further, it may be concluded that the primitive Actinopterygian ancestors, from which the various diverging groups have been derived, possessed lepidotrichia in which the segments bore a very close resemblance to the scales, in histological structure especially, fins provided with a complete edging of fulcral scales along the anterior border (fig. 54), and probably also fulcra along the dorsal edge of the tail. Concerning the presence of actinotrichia at the margin of the fins of the fossil forms, I have no direct evidence; but, judging from analogy, it may safely be concluded that such delicate rays were present also in the extinct Actinopterygians, and we may hope to discover remains of them in sections through well-preserved specimens.

Crossopterygii.

For our knowledge of the structure of this very heterogeneous group we are chiefly indebted to the works of Agassiz (1), Pander (27), Huxley (18, 19, and 20), Traquair (34 and 37 a), and A. S. Woodward (42). In the study of the fin-rays we meet with much greater diversity of form amongst these fish than amongst the Actinopterygians.

Real fulcral scales are not found in the Crossopterygii; nevertheless the dermal fin-rays at the front edge of the fins are often stronger and thicker than the others, and specialised large scales may be found at the base of the fins (figs. 50 and 51).

Osteolepidæ.—In this family the lepidotrichia resemble very closely those of the Palæoniscidæ. We find here the

same transition in form between the body-scales and the fin-ray segments at the anterior edge of the fin (fig. 51). But as a rule the distinction between the two is elsewhere marked and abrupt (fig. 56). So far as I have been able to observe, the proximal segment of the lepidotrichia of *Osteolepis*, although generally longer than the others, lies flush with the body-scales, and projects but very little below them. In the nearly allied *Diplopterus* the proximal end of the ray may be longer than in *Osteolepis* (fig. 56).

The lepidotrichia of the *Osteolepidæ* are covered with ganoine, and resemble closely the scales in histological structure.

Glyptopomidæ.—*Glyptopomus* (*Glyptolæmus*) has thin rhombic scales, ornamented with ganoine (Huxley, [19]). The ganoine scarcely shows in the fossils on the fins, where it was probably only feebly developed. The lepidotrichia differ from those of the *Osteolepidæ* in having a very much longer unjointed proximal segment, which was, perhaps, entirely, and certainly was partially, covered with ordinary scales. These scales become very thin and cycloid towards the periphery.

Rhizodontidæ.—*Eusthenopteron* and its allies differ from the *Osteolepidæ* in having thinner, deeply overlapping body-scales of more or less cycloid shape. Most of the genera, excepting *Gyroptychius*, seem to have lost the coating of ganoine on the lepidotrichia.

Taking *Eusthenopteron* as a type, we find well-developed lepidotrichia, freely branching and many-jointed (figs. 5 and 6). These rays are formed of bony substance, containing bone-cells (fig. 43). The bone is laid down in concentric layers in the proximal region, but as we pass towards the periphery of the fin we find that the segments get more and more flattened out, and become concave on their inner face. The distal segments in section appear crescentic, like those of modern Teleosts or *Pholidophorus* (figs. 45 A, B, and C). On comparing sections taken at various levels of the dermal ray, from within outwards, it will be seen that there is no fundamental difference between them, and that there is a gradual

transition from the rounded proximal segment to the more flattened distal segments (fig. 45).

On reaching the body the lepidotrichia are continued, each in a single elongated piece which passes beneath the scales and embraces the extreme end of the endo-skeletal fin-support (fig. 5). In the living fish the rays probably overlapped a certain amount of cartilage at the end of these bony endo-skeletal rays.

In *Gyroptychius*, which has preserved the ganoine covering on its lepidotrichia, the segments have the appearance of oblong shiny scales with a pitted surface. They closely resemble the lepidotrichia of *Osteolepis*. Unfortunately, the specimens I have examined are too fragmentary to allow of an exact determination of the relation the proximal end of the rays bears to the body-scales. Occasionally the appearance of the rays is such as to lead one to believe that they are formed, as Agassiz suggested for *Palæoniscus* (1, see p. 497), of ganoid scales overlapping deeper dermal rays. Pander, in fact, definitely states that this is the case not only in *Gyroptychius*, but also in *Osteolepis* (27). The same idea is suggested by some specimens of *Rhabdolepis macropterus*, Nevertheless I believe that the rays are not really double, and that the deceptive appearance is due to the breaking away of the superficial bony layers together with the outer ganoine.

Holoptychiidæ.—Passing now to this last family of the *Crossopterygii*, fish which, although they have preserved a considerable amount of ganoine, have acquired cycloid overlapping scales, we find lepidotrichia of essentially similar structure. In *Glyptolepis* the dermal rays closely resemble in their general proportions those of *Glyptopomus*. The lengthened proximal segment is perhaps a little shorter; it has no ganoine covering, and is of the same bony structure as the deep layers of the body-scales (fig. 44). The exposed jointed portions of the lepidotrichia are of similar bone, but are provided with a ganoine surface.

Holoptychius Flemingii is not well enough preserved

to allow of the histology being described. But it is a very interesting and important form, since its lepidotrichia are provided with proximal unjointed buried segments longer than those of any other Teleostome I have seen. The rays are very numerous and very slender. The whole of the long proximal segment was doubtless covered over by the body-scales, and must have overlapped the endo-skeletal rays to a considerable extent. The caudal fin of *Holoptychius* has been figured by A. Smith Woodward (42).

Osteolepis, *Diplopterus*, *Glyptolepis*, and *Holoptychius* represent so many stages in the development of the lepidotrichia. In which direction the evolution has progressed, whether from the rays with short superficial proximal segments to those with long deeply buried proximal segments, or vice versa, is a difficult point we shall have to discuss later (p. 509).

Cœlacanthidæ.—The dermal fin-rays of these fish have been described by Huxley (20), Reis (30), and other writers. It is well known that in the remarkable upper and lower lobes of the large caudal fin (not in the median lobe?) the dermal rays are regularly related to the endo-skeletal fin-supports, one pair to each, as in the higher *Actinopterygii*. Since the endo-skeleton of the other fins is not well preserved it is not possible to find out the exact relations of the dermal rays to the endo-skeleton, but they were almost certainly different. The dermal rays themselves are well-developed lepidotrichia, unbranched, and with a long proximal pointed segment overlapping the endo-skeleton (fig. 65 A). The joints in the distal region are very numerous, and very short and broad. Whilst the body-scales which cover the unsegmented region are provided with peculiar narrow spines, similar spines are found on the segments of the jointed region of the rays, and especially all along the edges of the fins (figs. 65 A and B). The spines must not be confused with the very similar fulcral scales of the *Actinopterygii* (fig. 54). They are not modified scales like the latter, but denticles of dentine, with perhaps a coating of enamel, homologous with the small denticles on the scales and dermal rays of *Lepidosteus*.

The lepidotrichia of the Cælacanthidæ are formed of normal bone, like those of other Crossopterygii.

Dipnoi.

We owe chiefly to Günther (12) and Traquair (34) the proper delimitation of this group, by the bringing together of the fossil allies of *Ceratodus*, which had previously been associated with the Crossopterygii. Not many genera of extinct Dipnoi are known, and of these only very few are sufficiently well preserved to afford any evidence with regard to the fin-rays. *Dipterus*, *Scaumenacia*, and the nearly allied *Phaneropleuron* are the only genera whose fins I have had the opportunity of studying in detail.¹

Scaumenacia has well-developed fin-membranes, supported by very numerous dermal rays, as shown by Whiteaves (41). Speaking generally, the dermal rays of this fish and of *Phaneropleuron* conform well to the type of ray found in *Ceratodus*, which I have named *camptotrich* (p. 486). They are long, slender, set very close together, and overlap proximally the whole of the first or distal segment of the endo-skeletal fin-support. The *camptotrichia* of *Scaumenacia* are subdivided into two regions of approximately equal length. The proximal half is in the form of a straight, rounded, unsegmented piece, which is covered over by the thin scales of the body (fig. 4). The distal half is often branched, has numerous and fairly regular articulations, and tapers gradually to the edge of the fin. As in Crossopterygians, whilst the transverse section of the proximal region of the dermal ray is circular, showing concentric lines of growth, it becomes more and more flattened distally, and also concave on its inner surface (figs. 33 A and B).

The bony substance of the *camptotrichia* contains many elongated bone-cells (fig. 42). Whether the body-scales extend over the fins of *Scaumenacia* as far as in *Ceratodus*, I

¹ I have to thank Dr. Traquair for the generous gift of a specimen of *Dipterus*. R.

am unable to say. The dermal rays of the paired fins are essentially similar to those of the median fins; but, of course, the proximal segment is shorter.

The dermal rays of *Dipterus* are extremely interesting. It will be remembered that in this ancient Dipnoan the median fins are of the discontinuous type found in *Crossopterygii*.¹ *Ceratodus*, *Ctenodus*, and *Uronemus* have a single continuous median fin, whilst *Phaneropleuron* has a separate anal, and *Scaumenacia* an anal and dorsal. *Dipterus* has separate short and powerful dorsal, caudal, and anal fins. Now Dollo has argued with great force that the progress of evolution in the Dipnoi has been from the *Dipterus* type to the *Ceratodus* type of median fin (9). There are, however, objections to this view, as we shall see later.

The scales of *Dipterus* are still cycloid, but they are thicker, and covered with a better developed layer of ganoine than in other Dipnoi. In many specimens the ganoine of the body-scales is not present, having probably been either broken off or destroyed in the process of fossilisation.

Pander has studied the dermal skeleton of the fins in detail. According to his account and figures, *Dipterus* is provided with bony, jointed, and branching rays, which are covered over with small superficial ganoid scales. Moreover he describes the jointed dermal rays as articulated to the extremity of corresponding proximal "Träger" (apparently meaning endo-skeletal fin-supports), which are also covered over with scales similar to those on the body (27). With regard to these proximal "Träger," there can be little doubt that they are merely the bases of the dermal rays.

After the most careful examination of as many specimens as possible, I have not been able to dispel all doubt from my mind as to the structure of the fins of *Dipterus*. In the majority of fossils they appear to be as follows:—The fin-membranes are supported by numerous dermal rays, on the

¹ It must not be forgotten, in view of the discussion which follows, that *Tarassius* is said to be a *Crossopterygian* with a continuous median fin.

whole quite similar to those of *Ceratodus*. They have a distal region, which is regularly jointed, and a proximal region without articulations (fig. 35). It is this region which Pander evidently mistook for the endo-skeletal fin-supports. The proximal unsegmented piece is covered over by the thick body-scales. In particularly well preserved fossils the segments can often be seen to be of very unequal length (this is, at all events, the case in *Dipterus macropterus*); they may be much shorter proximally than in the more distal region, as is the case in so many Teleostomes. Never is there to be seen on the rays the grooved and pitted surface and the ganoine layer characteristic of the superficial scales. The dermal rays are of essentially the same structure in all the fins, whether paired or unpaired (figs. 27 and 58).

On examining, in these specimens, the anterior edge of the second dorsal, the anal, and of the paired fins, and the lower edge of the caudal fin, we find series of small bright scales lying along the extreme edge of the fin and extending some way up the dermal rays (figs. 27 and 58). They have been indicated in the figures of *Dipterus* given by Huxley (18) and A. S. Woodward (42). These scales, of oval or oblong shape, are of considerable thickness, are covered with an external layer of ganoine, and ornamented with grooves and pits, just as is the case with the ordinary body-scales (fig. 28). They also resemble the body-scales and head-plates in histological structure (figs. 38 and 39). In fact, there can be no doubt that the fin-scales are homologous with the body-scales, and there can also be no doubt that they are not merely fuleral scales, comparable to those of the Actinopterygii. The small fin-scales just described undoubtedly lie at a higher level than the camptotrichia, which are below them. They appear to correspond in position and length with the segments of the rays, but are not articulated so close together end to end as are the consecutive segments of the underlying dermal rays. It is to be noticed also that they are much broader, and that whilst in the camptotrichia of *Dipterus*, and indeed to some extent of all Dipnoi, the articu-

lation is thicker than the middle region of each segment, in the case of the superficial fin-scales it is usually just the reverse, the middle region of the scale being the widest (figs. 57 and 58). The only doubtful point is as to whether they are, or are not, continuous below with the rays. I am strongly

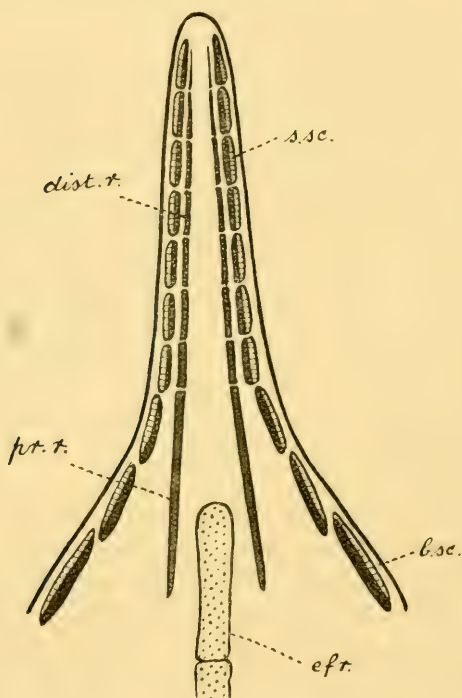


FIG. 6.—Diagrammatic section through the dorsal fin of *Dipterus*.
For lettering see p. 517.

of the opinion that they are not. A section of the fin showing the scales above and the camptotrichia below would, of course, clinch the argument in favour of Pander's view; but such a decisive section I have, unfortunately, not been able to obtain for lack of suitable material.

The dermal rays of *Dipterus* are formed of bone with numerous branching cells, very like those of *Ceratodus*

(fig. 40). Transverse sections of the proximal unsegmented region show that the bone is deposited in circular concentric layers, as in allied forms (fig. 32).

There are some specimens of *Dipterus* in which the ganoine is well preserved on the body-scales; and, as a rule, the fins in these fossils present a different appearance. Instead of a mere edging of scales at and near the margin of the fins, we find that the whole web of the fin is entirely covered with scales, similar to the marginal scales described above (figs. 57). These fin-scales have a pitted and ganoid surface, and are set in regular branching rows end to end. They are smaller distally than proximally, where they pass gradually into the ordinary form of scale covering the body. So far as my experience goes, in such fossils the jointed dermal ray itself cannot be seen. In fact, when the dermal rays are clearly visible the superficial scales are only seen near the margin of the fins; and vice versâ, when the general covering of scales is preserved the dermal rays do not appear. This peculiar condition of things may be due to some original difference between the various specimens of *Dipterus*, or, as seems much more probable, to a difference in the preservation of the fossils. Puzzles of this nature are familiar to those who study delicate fossils in detail.

It may, I think, be safely concluded that Pander was right in describing the fin-rays of *Dipterus* as covered with independent and more superficial scales, as shown in Text-fig. 6, p. 506.

Several important questions now suggest themselves. Firstly, are the jointed dermal rays homologous throughout the Dipnoi? Secondly, which is the more primitive condition, that of *Dipterus* or that of *Protopterus*? Thirdly, are all or any of the dermal rays of the Dipnoi homologous with those of other fish?

With regard to the first question, it may be pointed out that *Dipterus* on the one hand, and *Protopterus* (or *Lepidosiren*) on the other, represent the two extremes of structure in the dermal rays. *Scaumenacia* and *Ceratodus* are inter-

mediate forms uniting the one with the other. As we pass from *Dipterus* to *Scaumenacia* we see the dermal rays becoming longer, more slender, and more even in size. The segments also become longer and of approximately equal length throughout. In *Ceratodus* the rays become irregularly jointed and less branched; they tend to lose the calcification and to become more flexible and fibrous. Finally, in *Protopterus* the rays are cylindrical, fibrous, almost quite unjointed and unbranched structures, with little calcification and fewer bone-cells. The rays of *Protopterus* and *Lepidosiren* approach, in some respects, the ceratotrichia of *Elasmo-branchs*.

The transition is so gradual, and the relation of the proximal end of the dermal rays to the endo-skeleton and to the superficial covering of scales is so similar in all cases, that there can be little doubt that the dermal rays of these *Dipnoi* are homologous structures, to all of which the name *camptotrichia* may conveniently be applied.

The two next questions are too intimately connected to be treated separately.

Either we may assume that the *camptotrichia* of the *Dipnoi* are homologous with the ceratotrichia of the *Selachians*, and that the superficial covering of fin-scales corresponds to the basal plates of the denticles, and therefore also to those scales which have become converted into the lepidotrichia of the *Teleostomes* (p. 490); or we may suppose that the *camptotrichia* of the *Dipnoi* are homologous with the lepidotrichia of the *Teleostomes*, and have become covered over by a secondary extension of the scales of the body, as appears to have happened in the case of some *Teleosts* (p. 499).

On the first hypothesis the dermal rays of *Protopterus* or *Lepidosiren* would naturally be considered as the most primitive in the *Dipnoi*, since they most closely resemble the ceratotrichia. The rays of *Scaumenacia* and *Dipterus* would, on the contrary, be amongst the most specialised. Now if we appeal for evidence to the other parts of these fish, we find that their testimony points to an almost diametrically

opposed conclusion. Dollo (9) has strongly urged that *Scaumenacia*, *Ceratodus*, *Protopterus*, and *Lepidosiren* form a degenerating series. The structure of the skull, of the fins, of the scales, and of the respiratory and other internal organs of the living forms, all support this view. The evidence of the skull is especially strong, and has not, I venture to think, hitherto been quite rightly interpreted.

It is a question which I do not propose to discuss in detail in the present paper; but it may be pointed out that the series *Protopterus*, *Ceratodus*, *Ctenodus*, *Scaumenacia*, approaches nearer and nearer to the *Crossopterygian* type of skull in the conformation of its cranial roof. *Scaumenacia*, indeed (as I have myself observed), has an almost typical *Crossopterygian* roof, with large paired frontals and parietals meeting in the middle line, and not separated by median bones. So far, then, I am inclined to agree with Dollo, and believe that the evidence derived from the structure of the fin-rays supports his contention that the direction of specialisation has been from *Scaumenacia* or *Phaneropleuron* towards *Protopterus*.

For it must be remembered that although the *camptotrichia* of *Protopterus* and *Lepidosiren* bear a certain superficial resemblance to the *ceratotrichia* of *Elasmobranchs*, yet they differ from them in points which may well be considered as fundamental. As was shown above (p. 482), they are not homogeneous, they contain bone-cells, they are generally jointed, and are developed only in a single layer.

We have seen that the *Holoptychiidæ*, amongst the *Crossopterygii*, approach most nearly to the *Dipnoi* in the structure of their dermal rays, as they do also in their general anatomy. The *lepidotrichia* of *Glyptolepis* are not distinguishable in any important respect from the *camptotrichia* of *Scaumenacia* or *Ceratodus*. So strong is the resemblance that we are almost forced to believe that the dermal rays of the *Dipnoi* are only specialised forms of *lepidotrichia*.

If we adopt this view, and if at the same time we hold that

the lepidotrichia of the Teleostomes were themselves originally derived from scales, we are driven to admit that the scaling on the Dipnoan fin outside the dermal rays is of secondary and later origin, like the scaling on the head and fins of certain Teleostean fish (p. 491). We should then have two generations of dermal structures superimposed one above the other. That this interpretation is not improbably correct is evident when we reflect that in *Ceratodus* itself the dermal bones of the skull are, to a great extent, covered over by superficial scales similar to those on the body and fins.

To assign *Dipterus* to its proper taxonomic position is at present a most difficult matter. Judging from the structure of its cranial roof, it cannot be placed between *Scaumenacia* and the *Crossopterygii*. In *Dipterus* the frontals and parietals have apparently been reduced in size and pushed aside to accommodate the newly developed median bones. Were it not for its median fins, which in number and shape so closely resemble those of the Teleostomes, *Dipterus* would find a place near *Ctenodus* as a specialised offshoot from the main Dipnoan stem, in which the dermal skeleton had acquired a peculiarly thick coating of ganoine. According to the view set forth above, whilst the dermal rays of *Dipterus* are still quite similar to those of the *Crossopterygii*, the secondary outer scaling has been developed on the fins to a greater extent than in any other Dipnoan.

We have just examined the evidence in favour of the view that the Dipnoan camptotrichia were derived from lepidotrichia such as are found in the Teleostomes; we have also briefly disposed of the theory that the camptotrichia of the living Dipnoi were directly evolved from the ceratotrichia of Elasmobranchs. Let us now discuss a third possibility, that the dermal rays of the Teleostomes and Dipnoi are formed by the combination of the Elasmobranch ceratotrichia with the bony superficial scaling.

It may well be urged that the Dipnoi diverged from the Teleostome stem at a very early period indeed; that, consequently, those Teleostomi which most closely resemble

the Dipnoi, and those Dipnoi which most closely resemble the Teleostomi, are most likely to possess the most primitive type of dermal rays. Now *Phaneropleuron* or *Scaumenacia* on the one hand, and *Glyptolepis* or *Holoptychius* on the other, fulfil these conditions. It has been shown above that their dermal rays are of very similar character (p. 501). They are very numerous, closely packed, slender, elongated rods, tapering gradually towards the periphery, and branching occasionally, but not very much. They are provided with a long proximal unsegmented piece, deeply embedded in the body, overlapping the endo-skeletal fin-supports, and covered over by the body-scales. The bony nature of these rays may be considered as an expression of the general tendency, so to speak, of these fish towards the ossification of all their skeletal structures. The breaking up into joints of that portion of the ray which projects beyond the body might follow as a necessary consequence of the hardening through ossification.

According to this view, then, the ceratotrichia and the basal plates of the denticles of Elasmobranchs would be represented in the Dipnoi by the camptotrichia and the superficial scales.

But in the Teleostomi we must suppose that these two originally separate elements have become so closely connected that they have finally fused with each other, giving rise, in the web of the fin, to jointed dermal rays with scale-like upper surface. Each segment of the lepidotrich would thus have been formed by the combination of an elongated ganoid scale with a segment of the underlying bony ray. The proximal unjointed region of the ray, embedded in the body, and separated from the body-scales by a considerable thickness of soft tissues, would never have fused with the scales, and thus would acquire neither the joints nor the ganoine covering. The structure of *Glyptolepis*, perhaps one of the most primitive of the known Crossopterygians, and of *Cheirolepis*, the most ancient of Actinopterygians, would certainly agree most remarkably with this interpretation.

We should have further to imagine, to complete our theory, that the tendency amongst the Teleostomes has been for the proximal embedded portion of the ray to become shorter and shorter, until, in the higher Actinopterygii, it has practically disappeared, except in certain regions of the caudal fin. The dermal ray would then articulate, at the edge of the body, with the tip of the endo-skeletal fin-support.

The presence of actinotrichia, in addition to the lepidotrichia, would not be a serious objection, since there may have been several generations or layers of ceratotrichia in the ancestral form.

CONCLUSION.

To conclude, we may briefly summarise some of the facts dealt with above, and point out some of the difficulties which remain unsolved.

In all the fins of the true Pisces there are present dermal rays of mesoblastic origin, the dermatrichia. In the Elasmobranchii and Holocephali, and probably also in the Acanthodii and the Ichthyotomi, these rays are unjointed, occasionally branched, and composed of a fibrous substance of horny consistency without bone-cells. When denticles (placoid scales) are present they are quite independent of the rays, and more superficial in position. To these rays I propose to give the name ceratotrichia. Their origin is unknown, and for the present they must be considered as special developments of the connective tissue.

All living Teleostomes—that is to say, Polypterus (*Calamoichthys*?) and the Actinopterygii (Ganoids and Teleosts)—are provided with small, horny, unjointed rays at the edge of their fins, to which the name actinotrichia has been given. In the early stages of development these are the only dermal rays supporting the fins. Actinotrichia were probably present in the extinct Actinopterygii and Crossopterygii. These small rays appear to be vestigial structures homologous with the ceratotrichia.

The Teleostomi are further provided with jointed, and

branched, bony, dermal rays, developed outside the actinotrichia. They bear, in primitive forms, the closest resemblance to the body-scales, and I propose to call them the lepidotrichia. They have doubtless arisen through the modification of scales, which must have spread over the whole web of the fins. In the primitive Teleostomes the lepidotrichia are very numerous, and often extended into the body by means of a long proximal unjointed piece passing below the body-scales. This proximal segment is more developed in the Crossopterygii than in the Actinopterygii, and more developed in those Crossopterygii in which the tail is scarcely heterocercal, and in which the body-scales are more or less cycloid, than in the Osteolepidæ. It is best developed of all amongst those forms, like the Holoptychiidae, with acutely lobate paired fins.

In the Dipnoi are found jointed, branched, dermal rays, of bony substance, containing bone-cells. The name *camptotrichia* is provisionally given to these rays, which appear to be in a degenerate condition in the highly modified living forms *Lepidosiren* and *Protopterus*, and even to some extent in *Ceratodus*. The *camptotrichia* are always provided with a proximal unsegmented region, deeply embedded in the body and covered by the body-scales. Scales also extend over the whole or the greater part of the fins, overlying the dermal rays.

The evidence derived from a comparison of the Dipnoi with other fish appears to favour the view that the *camptotrichia* represent the lepidotrichia of the Teleostomes.

Assuming that the lepidotrichia have originated from modified scales, it may be held that the Dipnoi with their *camptotrichia* have been derived from ancestral forms with lepidotrichia, and that the rays have become somewhat degenerate, have sunk below the surface, and have become covered over by a secondary extension of the body-scales on to the fin, as seems to have happened quite independently in some Teleosts. Such early ancestors would presumably be Teleostomes with amphistylic skulls, a small hyomandibular,

cycloid scales, and acutely lobate fins. Of all known fish the Holoptychiidae would appear most likely to approach this intermediate type. But the adoption of this theory meets with serious difficulties. The presence of a proximal joint of considerable length extending below the body-scales in some Teleostomes (such as *Cheirolepis*) is not easy to account for; and the relation the inner ends of the ceratotrichia, camptotrichia, and lepidotrichia bear to the muscles, connective tissue, and endo-skeleton, is so similar in all fish that it is difficult to believe that all these rays have not been, at all events partly, derived from some common form.

According to the second and alternative theory, it may be supposed that the camptotrichia of the Dipnoi have been derived from the ceratotrichia of the Elasmobranchii, and that they are overlaid with scales as the horny fin-rays are overlaid with denticles. The jointing of the distal region of the rays would follow on their ossification. On such a view, it might be supposed that the lepidotrichia of the Teleostomes have been formed by the fusion of the original dermal rays with the superficial scales in the distal region, but not in the proximal region, where the rays were deeply embedded and remain unjointed.

From a compound dermal ray so formed the lepidotrichia of the higher Actinopterygii would be derived by the shortening of the proximal piece. The structure of the rays of *Cheirolepis*, and many of the Crossopterygii (Holoptychiidae especially), may be taken as strong evidence in favour of this second theory. But here, again, we meet with many difficulties, such as the structure of the dermal rays of the Osteolepidae, in which the proximal piece is scarcely developed.

Between these two rival theories it is difficult, if not impossible, to choose in our present state of knowledge. I have endeavoured above to give an impartial statement of the two possible interpretations; but it may be added that I am strongly inclined to believe that the first theory is the one which is nearest the truth.

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EXPLANATION OF PLATES 35—41,

Illustrating Mr. Edwin S. Goodrich's paper "On the Dermal Fin-rays of Fishes—Living and Extinct."

LIST OF REFERENCE LETTERS.

Act. Actinotrichia. *b.c.* Bone cell. *b.m.* Basement membrane. *b.s.* Bony segment. *b.sc.* Body-scale. *c.* Canal. *cnt.* Connective tissue. *c.s.* Cut surface. *ct.* Ceratotrichia. *d.* Denticle. *d.c.* Distal cartilage. *dist.s.* Distal segment of dermal ray. *d.r.* Distal region of dermal ray. *d.s.e.* Distal segment of endo-skeletal ray, exposed. *e.f.* Edge of fin. *e.f.r.* Endo-skeletal fin-ray. *ep.* Epidermis. *fulc.* Fulcral scale. *g.r.* External layer of ganoine. *hyp.* Hypural cartilage or bone. *i.b.r.* Inner bony region. *i.f.r.* Inner fibrous region. *iptm.* Inner pterygial muscles. *i.r.* Inner region. *i.s.s.* Impression of superficial scale. *j.* Joint. *kpt.* Kamptotrichia. *lept.* Lepidotrichia. *lig.* Ligament. *m.* Stony matrix. *ms.* Muscle. *m.sc.* Median scale. *n.* Nucleus. *nt.* Notochord. *o.b.r.* Outer bony region. *op.* External opening of bone canal. *optm.* Outer pterygial muscles. *o.r.* Outer region. *p.r.* Proximal region. *pr.s.* Proximal segment. *sc.* Scale. *sk.* Skin. *sm.sc.* Small scales overlying dermal rays. *s.s.* Superficial scale.

PLATE 35.

FIG. 1.—Portion of the first dorsal fin of *Scyllium canicula* cut off and dissected on the left side so as to show the relations the skin, muscles, dermal rays, and endo-skeletal rays bear to each other. Slightly diagrammatic and enlarged.

FIG. 2.—Similar view of a portion of the dorsal fin of *Acipenser sturio*.

FIG. 3.—Similar view of a portion of the ventral region of the caudal fin of *Ceratodus Forsteri*.

FIG. 4.—Three endo-skeletal fin-supports and some dermal fin-rays of the second dorsal fin of *Scaumenacia curta*. The distal end of the lowest endo-skeletal ray has been exposed by the removal of the covering dermal rays. Slightly diagrammatic and enlarged.

FIG. 5.—Enlarged and somewhat diagrammatic view of the anterior region of the large dorsal lobe of the caudal fin of *Eusthenopteron Foordi*, showing the relation of the dermal rays to the body-scales and endo-skeletal fin-supports.

FIG. 6.—Enlarged view of a small part of a dermal ray of the same *Eusthenopteron*.

PLATE 36.

FIG. 7.—Small portion of a transverse section through the ventral lobe of the caudal fin of an embryo *Scyllium canicula*, 80 mm. long, showing the ceratotrichia, the connective-tissue layers, and the developing denticles. Cam. $\times 300$.

FIG. 8.—Section through the skin of the caudal fin of an embryo *Scyllium canicula*, 23 mm. long, cutting a little obliquely through the developing ceratotrichia. Cam. oil im., oc. 8.

FIG. 9.—Section through the ventral lobe of the caudal fin of an embryo *Scyllium canicula*, 80 mm. long, cutting the ceratotrichia longitudinally. Cam. $\times 450$.

FIG. 10.—Similar section nearer the edge of the fin, and cutting the ceratotrichia across. Cam. $\times 300$.

FIG. 11.—Section of the ventral lobe of the caudal fin of an embryo *Scyllium canicula*, 60 mm. long, cutting across the ceratotrichia. Cam. $\times 300$.

FIG. 12.—Similar section of the fin of an embryo *Scyllium canicula*, 23 mm. long. Cam. $\times 300$.

FIGS. 13—15.—Sections through the same dorsal fin of a young *Protopterus*, cutting across the dermal rays. The section represented in Fig. 13 is nearest the edge, and that in Fig. 15 nearest the base of the fin. Cam. $\times 300$.

FIG. 16.—Similar section through the same fin near its base, showing the developing scales. Cam. $\times 300$.

PLATE 37.

FIG. 17.—Section through the distal region of the pelvic fin of *Polypterus lapradii*, showing the actinotrichia, and the lepidotrichia developing as a thickening of the basement membrane. Cam. $\times 350$.

FIG. 18.—Section nearer the base of the same fin. The lepidotrichia are here thick, bony, and armed with denticles. $\times 80$.

FIG. 19.—Section through the distal region of the pectoral fin of *Lepidosteus osseus*, showing the actinotrichia and the young lepidotrichia cut across. Cam. $\times 350$.

FIGS. 20—23.—Sections through the caudal fin of a young trout, *Salmo fario*, 21 mm. long. The sections pass progressively nearer the base of the fin, Fig. 20 representing that nearest the edge. The developing lepidotrichia are cut through transversely. Cam. $\times 700$.

FIG. 24.—Approximately longitudinal section through the developing actinotrichia and lepidotrichia, taken from the caudal fin of a young *Salmo fario*, 45 mm. long. Cam. $\times 700$.

FIG. 25.—Transverse section through the proximal region of the caudal fin of a young *Salmo fario*, 21 mm. long. Cam. $\times 45$.

FIG. 26.—Transverse section through the base of the anterior dorsal fin of the same fish.

PLATE 38.

FIG. 27.—A few of the dermal rays and superficial scales of the pelvic fin of *Dipterus valenciennesi* (No. P. 618 of the British Museum). Enlarged.

FIG. 28.—Still more enlarged view of a small portion of the same.

FIG. 29.—Enlarged view of small portions of the dermal rays of the pelvic fin of *Ceratodus Forsteri*.

FIG. 30.—Transverse section through the ventral lobe of the caudal fin of a young *Protopterus*. Cam. $\times 40$.

FIG. 31.—Longitudinal section through the dermal ray of the same *Protopterus*, showing the inner and outer layers. Cam. $\times 400$.

FIG. 32.—Transverse section through the proximal unjointed region of the dermal rays of the anal fin of *Dipterus valenciennesi*. Cam. $\times 110$.

FIG. 33A.—Transverse section through the proximal unjointed region of the dermal rays of the ventral lobe of the caudal fin of *Scaumenacia curta*. Cam. $\times 80$.

FIG. 33B.—Section of the distal segmented region of the same. Cam. $\times 80$.

FIG. 34.—Transverse section through the distal jointed region of the dermal rays of the pectoral fin of *Ceratodus Forsteri*. Cam. $\times 80$.

FIG. 35A.—Enlarged view of two dermal rays from the anal fin of *Dipterus macropterus*.

FIG. 35B.—Still further enlarged view of a few segments of the distal region of the same.

FIG. 36.—Two dermal rays from the caudal fin of *Ceratodus Forsteri*. Slightly enlarged.

FIG. 37.—Three dermal rays from the pectoral fin of the same fish. Slightly enlarged.

FIG. 38.—Small piece from the surface of one of the superficial scales overlying the dermal rays of the median fin of *Dipterus valenciennesi*. Cam. \times 350.

FIG. 39.—Similar piece from a cranial shield of the same. Cam. \times 350.

PLATE 39.

FIG. 40.—Fragment of the dermal ray of *Dipterus valenciennesi*. Cam. \times 350.

FIG. 41.—Fragment of the dermal ray of *Ceratodus Forsteri*. Cam. \times 200.

FIG. 42.—Fragment of the proximal region of the dermal ray of *Scaumenacia curta*. Cam. \times 450.

FIG. 43.—Fragment of the distal region of the dermal ray of *Eusthenopteron Foordi*. Cam. \times 200.

FIG. 44.—Fragment of the proximal region of the dermal ray of *Glyptolepis* (British Museum, No. P. 3258).

FIG. 45A.—Transverse section through the proximal unjointed piece of the dermal ray of the ventral caudal lobe of *Eusthenopteron Foordi*.

FIG. 45B.—The same, cut through the more distal jointed region.

FIG. 45C.—The same, near the edge of the fin. All Cam. \times 80.

FIG. 46.—Transverse section through the jointed region of three dermal rays of *Cheirolepis traillii*. Cam. \times 80.

FIG. 47.—Transverse section through the proximal piece of the dermal rays and the overlying scales of the same fossil. Cam. \times 80.

PLATE 40.

FIG. 48.—Longitudinal section through the distal jointed region of the dermal rays of the same fossil, *Cheirolepis*. Cam. \times 80.

FIG. 49A.—Somewhat diagrammatic and enlarged view of the dermal rays of the caudal fin of *Cheirolepis traillii*. The superficial scales have been removed from over the proximal piece, and the ganoine covering from the segments of the distal region of three of the rays.

FIG. 49B.—Some body-scales of the same, enlarged.

FIG. 50.—Somewhat diagrammatic and enlarged view of the distal region of three lepidotrichia, reaching the edge of the anal fin, of *Osteolepis macrolepidotus*.

FIG. 51.—Enlarged view of the anterior edge of the base of the first dorsal fin of *Osteolepis macrolepidotus*, showing the transition between the segments of the lepidotrichia and the body-scales.

FIG. 52.—A touched-up enlarged photograph of a portion of the caudal fin of *Palæoniscus* sp.

FIG. 53.—Enlarged view of the proximal region of the ventral caudal lobe of tail fin of *Palæoniscus Freieslebeni*, showing how the dermal rays pass below the body-scales.

FIG. 54.—Enlarged view of three segments of the dermal ray at the anterior edge of the same fin.

FIG. 55A.—Outline of the tail of *Amblypterus Blainvilli*, shaded to show the region represented in Fig. 55B.

FIG. 55B.—Small portion of the caudal fin of the same, enlarged to show the perfect transition between the body-scales and the joints of the lepidotrichia.

FIG. 56.—Small portion of the caudal fin of *Diplopterus Agassizii*, enlarged to show the relation of the lepidotrichia of the ventral lobe to the body-scales.

FIG. 57.—Small portion of the second dorsal fin of *Dipterus valenciennesi*, enlarged. One half represents the outer surface of the covering scales, and the other half the impression left in the matrix by the scales of the opposite side.

FIG. 58.—Enlarged view of a portion of the lower edge of the anal fin of a *Dipterus valenciennesi*, showing the dermal rays and overlying scales. From a photograph touched up.

PLATE 41.

FIG. 59.—Portion of the lower half of the caudal fin of a salmon, *Salmo salar*, dissected so as to show the relation of the hypural bones to the dermal rays, two of which have been cut short at their proximal ends.

FIG. 60.—Small piece of a lepidotrich from the pelvic fin of *Polypterus*, superficial view.

FIG. 61.—Small piece of a lepidotrich from the anal fin of *Polypterus bichir*, showing the deep-lying canals in the bone, and the bone-cells.

FIG. 62.—Transverse section through the distal region of the lepidotrichia of the caudal fin of *Pholidophorus* sp. Cam. L. 4, oc. 3.

FIG. 63.—Fragment of the same. Cam. $\times 150$.

FIG. 64.—Fragment of a scale of *Pholidophorus*. Cam. $\times 150$.

FIG. 65A.—Distal segment of the endo-skeletal fin-support of the dorsal caudal fin of *Undina penicillata*, with its related dermal ray. Enlarged and somewhat diagrammatic.

FIG. 65B.—Small portion of a dermal ray of the same, showing the spine-like denticles, much enlarged.

FIG. 66.—Section through the caudal fin of *Hæmulon Seudderi*, cutting across the dermal rays near the edge of the fin. Cam. Enlarged.

FIG. 67.—Section through the same, cutting the dermal rays longitudinally and nearer the base of the fin. The separate overlying scales are here well shown. Cam. Enlarged.

The Structure and Classification of the Arthropoda.

By

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With Plate 42.

[By the great kindness of the proprietors of the tenth edition of the 'Encyclopædia Britannica' I have received permission to reprint in this journal the articles ARTHROPODA and ARACHNIDA, which I contributed to its pages. I have been anxious that morphologists should consider the views which I have put forward in these articles (written now nearly four years ago). At the same time I have observed that they have entirely escaped the notice of two authors who have recently written general essays on the Arthropoda, viz. Dr. A. S. Packard, of Salem, Mass., and Mr. G. H. Carpenter, of Dublin. I have revised both articles only in regard to verbal inaccuracies, excepting where I have definitely stated that new matter is introduced. I hope that in their present form these articles will not fail to come under the notice of zoologists.—E. R. L.]

ARTHROPODA is the name of one of the three sub-phyla into which one of the great phyla (or primary branches) of

cœlomocœlous animals—the Appendiculata—is divided, the other two being respectively the Chætopoda and the Rotifera. The word “Arthropoda” was first used in classification by Siebold and Stannius (*Lehrbuch der vergleich. Anatomie*,¹ Berlin, 1845) as that of a primary division of animals, the others recognised in that treatise being Protozoa, Zoophyta, Vermes, Mollusca, and Vertebrata. The names Condylopoda and Gnathopoda have been subsequently proposed for the same group. The word refers to the jointing of the chitinised exo-skeleton of the limbs or lateral appendages of the animals included, which are, roughly speaking, the Crustacea, Arachnida, Hexapoda (so-called “true insects”), Centipedes, and Millipedes. This primary group was set up to indicate the residuum of Cuvier’s Articulata when his class Annelides (the modern Chætopoda) was removed from that “embranchement.” At the same time Siebold and Stannius renovated the group Vermes of Linnæus, and placed in it the Chætopods and the parasitic worms of Cuvier, besides the Rotifers and Turbellarian worms.¹

¹ As a matter of fact the group Arthropoda itself, thus constituted, was precisely identical in its area with the class Insecta of Linnæus, the Entoma of Aristotle. But by causes which it is not easy to trace the word “Insect” had become limited since the days of Linnæus to the Hexapod Pterygote forms, to the exclusion of his Aptera. Lamarck’s penetrating genius is chiefly responsible for the shrinkage of the word Insecta, since it was he who, forty years after Linnæus’s death, set up and named the two great classes Crustacea and Arachnida (included by Linnæus under Insecta as the order “Aptera”) assigning to them equal rank with the remaining Insecta of Linnæus, for which he proposed the very appropriate class-name “Hexapoda.” Lamarck, however, appears not to have insisted on this name Hexapoda, and so the class of Pterygote Hexapods came to retain the group-name Insecta, which is, historically or etymologically, no more appropriate to them than it is to the classes Crustacea and Arachnida. The tendency to retain the original name of an old and comprehensive group for one of the fragments into which such group becomes divided by the advance of knowledge—instead of keeping the name for its logical use as a comprehensive term, including the new divisions, each duly provided with a new name—is most curiously illustrated in the history of the word Physiology. Cicero says, “Physiologia naturæ ratio,” and such was the meaning of the name Physiologus, given to a

The result of the knowledge gained in the last quarter of the nineteenth century has been to discredit altogether the group *Vermes*, thus set up and so largely accepted by German writers even at the present day. We have, in fact, returned very nearly to Cuvier's conception of a great division or branch, which he called *Articulata*, including the *Arthropoda* and the *Chaetopoda* (the latter equivalent to the *Annelides* of Lamarck, a name adopted by Cuvier), and differing from it only by the inclusion of the *Rotifera*. The name *Articulata*, introduced by Cuvier, has not been retained by subsequent writers. The same, or nearly the same assemblage of animals has been called *Entomozoaria* by De Blainville (1882), *Arthrozoa* by Burmeister (1843), *Entomozoa* or *Anellata* by Milne-Edwards (1855), and *Annulosa* by M'Leay (1819), who was followed by Huxley (1856). The character pointed to by all these terms is that of a ring-like segmentation of the body. This, however, is not the character to which we now ascribe the chief weight as evidence of the genetic affinity and monophyletic (uni-ancestral) origin of the *Chaetopods*, *Rotifers*, and *Arthropods*. It is the existence in each ring of the body of a pair of hollow lateral appendages or *parapodia*, moved by intrinsic muscles and penetrated by blood-spaces, which is the leading fact indicating the affinities of these great sub-phyla, and uniting them as blood relations. The *parapodia* (fig. 7) of the marine branchiate worms are the same things genetically as the "legs" of *Crustacea* and insects (figs. 9 and 10). Hence the term *Appendiculata* was introduced by Lankester

cyclopædia of what was known and imagined about earth, sea, sky, birds, beasts, and fishes, which for a thousand years was the authoritative source of information on these matters, and was translated into every European tongue. With the revival of learning, however, first one and then another special study became recognised—*anatomy*, *botany*, *zoology*, *mineralogy*, until at last the great comprehensive term *Physiology* was bereft of all its once-included subject-matter excepting the study of vital processes pursued by the more learned members of the medical profession. Professional tradition, and an astute perception on their part of the omniscience suggested by the terms, have left the medical men in English-speaking lands in undisturbed but illogical possession of the words *physiology*, *physic*, and *physician*.

(preface to the English edition of Gegenbaur's 'Comparative Anatomy,' 1878) to indicate the group. The relationships of the Arthropoda thus stated are shown in the subjoined table :

Phylum APPENDICULATA	{	Sub-phylum 1. Rotifera.
		„ 2. Chætopoda.
		„ 3. Arthropoda.

The Rotifera are characterised by the retention of what appears in Molluscs and Chætopods as an embryonic organ, the velum or ciliated præoral girdle, as a locomotor and food-seizing apparatus, and by the reduction of the muscular parapodia to a rudimentary or non-existent condition in all present surviving forms except Pedalion. In many important respects they are degenerate—reduced both in size and elaboration of structure.

The Chætopoda are characterised by the possession of horny epidermic chætæ embedded in the integument and moved by muscles. Probably the chætæ preceded the development of parapodia, and by their concentration, and that of the muscular bundles connected with them at the sides of each segment, led directly to the evolution of the parapodia. The parapodia of Chætopoda are never coated with dense chitin, and are, therefore, never converted into jaws; the primitive "head-lobe" or prostomium persists, and frequently carries eyes and sensory tentacles. Further, in all members of the sub-phylum Chætopoda the relative position of the prostomium, mouth, and peristomium or first ring of the body retains its primitive character. We do not find in Chætopoda that parapodia, belonging to primitively post-oral rings or body-segments (called "somites," as proposed by H. Milne-Edwards), pass in front of the mouth by adaptational shifting of the oral aperture. (See, however, 8.)

The Arthropoda might be better called the "Gnathopoda," since their distinctive character is that one or more pairs of appendages behind the mouth are densely chitinised and turned (fellow to fellow on opposite sides) towards one

another so as to act as jaws. This is facilitated by an important general change in the position of the parapodia; their basal attachments are all more ventral in position than in the Chaetopoda, and tend to approach from the two sides towards the mid-ventral line. Very usually (but not in the Onychophora = Peripatus) all the parapodia are plated with chitin secreted by the epidermis, and divided into a series of joints—giving the “arthropodous” or hinged character.

There are other remarkable and distinctive features of structure which hold the Arthropoda together, and render it impossible to conceive of them as having a polyphyletic origin,—that is to say, as having originated separately by two or three distinct lines of descent from lower animals; and, on the contrary, establish the view that they have been developed from a single line of primitive Gnathopods which arose by modification of parapodiate annulate worms not very unlike some of the existing Chaetopods. These additional features are the following:—(1) All existing Arthropoda have an ostiate heart and have undergone “phlebædesis,” that is to say, the peripheral portions of the blood-vascular system are not fine tubes as they are in the Chaetopoda and as they were in the hypothetical ancestors of Arthropoda, but are swollen so as to obliterate to a large extent the coelom, whilst the separate veins entering the dorsal vessel or heart have coalesced, leaving valvate ostia (see Fig. 1*) by which the blood passes from a pericardial blood-sinus formed by the fused veins into the dorsal vessel or heart (see Lankester’s ‘Zoology,’ part ii, introductory chapter; A. and C. Black, 1900). The only exception to this is in the case of minute degenerate forms where the heart has disappeared altogether. The rigidity of the integument caused by the deposition of dense chitin upon it is intimately connected with the physiological activity and form of all the internal organs, and is undoubtedly correlated with the total disappearance of the circular muscular layer of the body-wall present in Chaetopods. (2) In all existing Arthropoda the

region in front of the mouth is no longer formed by the primitive prostomium or head-lobe, but one or more segments, originally post-oral, with their appendages have passed in front of the mouth (prosthomeres). At the same time the prostomium and its appendages cease to be recognisable as distinct elements of the head. The brain no longer consists solely of the nerve-ganglion mass proper to the prostomial lobe, as in Chætopoda, but is a composite (syncerebrum) produced by the fusion of this and the nerve-ganglion masses proper to the prosthomeres or segments which pass forwards, whilst their parapodia (= appendages)

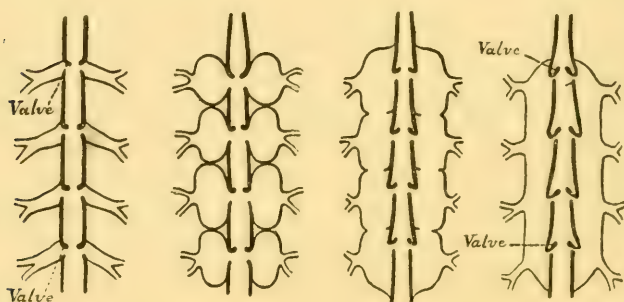


FIG. 1*.—Diagram to show the gradual formation of the Arthropod pericardial blood-sinus and "ostiate" heart by the swelling up (phlebædesis) of the veins entering the dorsal vessel or heart of a Chætopod-like ancestor. The figure on the left represents the condition in a Chætopod, that on the right the condition in an Arthropod; the other two are hypothetical intermediate forms. (After Lankester, 'Quart. Journ. Micr. Sci.,' vol. xxxiv, 1893.)

become converted into eye-stalks and antennæ, or more rarely grasping organs. (3) As in Chætopoda, cœlomic funnels (cœlomoduets) may occur right and left as pairs in each ring-like segment or somite of the body, and some of these are in all cases retained as gonoduets and often as renal excretory organs (green glands, coxal glands of Arachnida—not crural glands, which are epidermal in origin); but true nephridia, genetically identical with the nephridia of earthworms, do not occur (on the subject of

cœlom, cœlomoduets, and nephridia, see the introductory chapter of part ii of Lankester's 'Treatise on Zoology').

Tabular Statement of the Grades, Classes, and Sub-classes of the Arthropoda.—It will be convenient now to give in the clearest form a statement of the larger subdivisions of the Arthropoda which it seems necessary to recognise at the present day. The justification of the arrangement adopted will form the substance of the rest of the present article. The orders included in the various classes are not discussed here, but are treated of under the following titles:—PERIPATUS (Onychophora), MYRIAPODA (Diplopoda and Chilopoda), ARACHNIDA, INSECTA (Hexapoda), and CRUSTACEA.

SUB-PHYLUM ARTHROPODA (of the Phylum Appendiculata).

Grade A. **Hyparthropoda** (hypothetical forms connecting ancestors of Chætopoda with those of Arthropoda).

Grade B. **Protarthropoda**.

Class ONYCHOPHORA.

Ex.—Peripatus.

Grade C. **Euarthropoda**.

Class 1. DIPLOPODA.

Ex.—Julus.

Class 2. ARACHNIDA.

Grade *a*. Anomomeristica.

Ex.—Phacops.

Grade *b*. Nomomeristica.

(*a*) Pantopoda.

Ex.—Pycnogonum.

(*b*) Euarachnida.

Ex.—Limulus, Scorpio, Mygale, Aca-
rus.

Class 3. CRUSTACEA.

Grade *a.*—Entomostraca.Ex.—*Apus*, *Branchipus*, *Cyclops*, *Balanus*.Grade *b.* Malacostraca.Ex.—*Nebalia*, *Astacus*, *Oniscus*, *Gammarus*.

Class 4. CHILOPODA.

Ex.—*Scolopendra*.Class 5. HEXAPODA (syn. *Insecta Pterygota*).Ex.—*Locusta*, *Phryganea*, *Papilio*, *Apis*,
Musca, *Cimex*, *Lucanus*, *Machilis*.Incertæ sedis.—*Tardigrada*, *Pentastomidæ* (degenerate forms).

The Segmentation of the Body of Arthropoda.—The body of the Arthropoda is more or less clearly divided into a series of rings, segments, or somites, which can be shown to be repetitions one of another, possessing identical parts and organs which may be larger or smaller, modified in shape or altogether suppressed in one somite as compared with another. A similar constitution of the body is more clearly seen in the Chaetopod worms. In the Vertebrata also a repetition of units of structure (myotomes, vertebrae, etc.)—which is essentially of the same nature as the repetition in Arthropods and Chaetopods, but in many respects subject to peculiar developments—is observed. The name “metamerism” has been given to this structural phenomenon because the “meres,” or repeated units, follow one another in line. Each such “mere” is often called a “metamere.” This is not the place in which to discuss the origin and essential nature of “metamerism” or “metameric segmentation.” Nevertheless a satisfactory consideration of the structure of the Arthropoda demands a knowledge of what may be called the laws of metamerism. These are not so fully ascertained or formulated as might be expected. The repetition of parts, which we note as metamerism, is, as Haeckel, Bateson, and others have recognised, only a special

case of a tendency of the organic body to repetition of structural units or parts which finds one expression in bilateral symmetry. In certain worms (the Cestoidea and some Planarians) metameric segmentation is accompanied by the separation of the completed metameres one by one from the older (anterior) extremity of the chain (strobilation), but it by no means follows that metameric segmentation has a necessary origin in such completion and separation of the "meres." On the contrary, metamerism seems to arise from a property of organisms which is sometimes more (eumetagenesis) and sometimes less (dysmetagenesis) fully exhibited, and in some groups not exhibited at all. The most complete and, at the same time, simplest instances of metameric segmentation are to be seen in the larger Chaetopods, where some hundreds of segments succeed one another—each practically indistinguishable in structure from the segment in front or from that behind; muscles, right and left appendage or parapodium, colour pattern of the skin, gut, blood-vessels, coelom, nephridia, nerve-ganglion, and nerves are precisely alike in neighbouring segments. The segment which is least like the others is the first, for that carries the mouth and a lobe projecting beyond it—the prostomium. If (as sometimes happens) any of the hinder segments completes itself by developing a prostomium, the chain breaks at that point, and the segment which has developed a prostomium becomes the first or head-bearing segment of a new individual. Compare such an instance of metameric segmentation with that presented by one of the higher Arthropods—e. g. the crayfish. Here the somites are not so clearly marked in the tegumentary structures; nevertheless, by examining the indications given by the paired parapodia, we find that there are twenty-one somites present—a limited definite number which is also the precise number found in all the higher Crustacea.

We can state as a FIRST LAW¹ of metamerism or somite formation that it is either indefinite in regard to number of

¹ The word "LAW" is used in this summary merely as a convenient heading for the statement of a more or less general proposition.

metameres or somites produced or is definite. Animals in the first case we call anomomeristic; those in the second case, nomomeristic. The nomomeristic condition is a higher development, a specialisation, of the anomomeristic condition.

The SECOND LAW, or generalisation, as to metamerism which must be noted is that the meres or somites (excepting the first with its prostomium) may be all practically alike, or may differ from one another greatly by modification of the various constituent parts of the mere or somite. Metamerised animals are either homœomeric or heteromeric. The reference to the variation in the form of the essential parts contained in a "metamere" or "somite" introduces us to the necessity of a general term for these constituent or subordinate parts; they may be called "meromes" (*μέρος*). The meromes present in a metamere or somite differ in different annulate or segmented animals according to the general organisation of the group to which the animal belongs. As a matter of convenience we distinguish in the Arthropod as meromes, first, the tegumentary chitinised plates called terga, placed on the dorsal aspect of the somites; second, the similar sternal plates. In Chætopods we should take next to these the masses of circular and longitudinal muscular fibres of the body-wall and the dorso-ventral muscles. The latter form the third sort of merome present in the Arthropods. The fourth kind of merome is constituted by the parapodia or appendages; the fifth by the cœlomic pouches and their ducts and external apertures (cœlomo-ducts), whether renal or genital. The sixth by the blood-vessels of the somite; the seventh by the bit of alimentary tract which traverses it; and the eighth by the neuromere (nerve-ganglion pair, commissures, connectives, and nerve branches).

It becomes apparent from this enumeration that there are a good many important elements or "meromes" in an Arthropod metamere or somite which can become the subject of heteromerism, or, to use a more apt word, of "heterosis." It is all the more necessary to insist upon this, inasmuch as there is a tendency in the discussion of the segmentation of the

Arthropod body to rely exclusively upon the indications given by the tegumentary chitinous plates and the parapodia.

The THIRD LAW of metamerism is that heteromerism may operate in such a way as to produce definite regions of like modification of the somites and their appendages, differing in their modification from that observed in regions before and behind them. It is convenient to have a special word for such regions of like meres, and we call each a tagma (*τάγμα*, a regiment). The word "tagmosis" is applicable to the formation of such regions. In the Chætopods tagmosis always occurs to a small extent, so as to form the head. In some Chætopods, such as Chætopterus and the sedentary forms, there is marked tagmosis, giving rise to three or even more tagmata. In Arthropods, besides the head, we find very frequently other tagmata developed. But it is to be noted that in the higher members of each great class or line of descent, the tagmosis becomes definite and characteristic just as do the total number of meres or somites, whilst in the lower grades of each great class we find what may be regarded as varying examples of tentative tagmosis. The terms nomotagmic and anomotagmic are applicable with the same kind of implication as the terms nomomeristic and anomomeristic.

The FOURTH LAW of metamerism (auto-heterosis of the meromes) is that the meromes of a somite or series of somites may be separately and dissimilarly affected by heteromerism. It is common enough for small changes only to occur in the inner visceral meromes, whilst the appendages and terga or sterna are largely changed in form. But of equal importance is the independent "heterosis" of these visceral meromes without any corresponding heterosis of the body-wall. As instances we may cite the gizzards of various earthworms, and the special localisation of renal, genital, and gastric meromes, with obliteration elsewhere, in a few somites in Arthropoda.

The FIFTH LAW, relating also to the independence of the meromes as compared with the whole somite, is the law of autorhythmus of the meromes. Metamerism does not always

manifest itself in the formation of complete new segments; but one merome may be repeated so as to suggest several metameres, whilst the remaining meromes are, so to speak, out of harmony with it and exhibit no repetition. Thus in the hinder somites of the body of *Apus* the Crustacean we find a series of segments corresponding apparently each to a complete single somite, but when the appendages are examined we find that they have multiplied without relation to the other meromes of a somite; we find that the somites carry from two to seven pairs of appendages, increasing in number as we pass backwards from the genital segment. The appendages are autorhythmic meromes in this case. They take on a quasi-independent metamerism, and are produced in numbers which have no relation to the numbers of the body-rings, muscles, and neuromeres. This possibility of the independent metameric multiplication of a single merome must have great importance in the case of dislocated meromes, and no doubt has application to some of the metameric phenomena of Vertebrates.

A case which appears at first sight to be one of "autorhythmus" of the parapodia is that of the Diplopods (*Julus*, etc.), in which each apparent somite carries two pairs of legs or parapodia. It looks at first as though this were due to the independent multiplication of the legs; but it is not. Contrary to what obtains in *Apus*, we find in *Julus* that there is a well-marked somite in the embryo corresponding to each pair of legs, and that the adult condition arises from a fusion of the tegumentary meromes of adjacent somites (see below, "Fusion").

The SIXTH LAW is the law of dislocation of meromes. This is a very important and striking phenomenon. A merome, such as a pair of appendages (*Araneæ*) or a neuromere, or a muscular mass (frequent), may (by either a gradual or sudden process, we cannot always say which) quit the metamere to which it belongs, and in which it originated, and pass by actual physical transference to another metamere. Frequently this new position is at a distance of several metameres from

that to which the wandering merome belongs in origin. The movement is more usual from behind forwards than in the reverse direction ; but this probably has no profound significance, and depends simply on the fact that, as a rule, the head must be the chief region of development on account of its containing the sense organs and the mouth.

In the Vertebrata the independence of the meromes is more fully developed than in other metamerised animals. Not only do we get auto-heterosis of the meromes on a most extensive scale, but the dislocation of single meromes and of whole series (tagmata) of meromes is a common phenomenon. Thus in fishes the pelvic fins may travel forwards to a thoracic and even jugular position in front of the pectoral fins ; the branchiomeromes lose all relation to the position of the meromes of muscular, skeletal, cœlomic, and nervous nature, and the heart and its vessels may move backwards from their original metameres in higher Vertebrates carrying nerve-loops with them.

The SEVENTH LAW of metamerism is one which has been pointed out to the writer by Mr. E. S. Goodrich, of Merton College, Oxford. It may be called the law of "translation of heterosis." Whilst actual physical transference of the substance of meromes undeniably takes place in such a case as the passage of the pelvic fins of some fishes to the front of the pectorals, and in the case of the backward movement of the opisthosomatic appendages of spiders, yet the more frequent mode in which an alteration in the position of a specialised organ in the series or scale of metameres takes place is not by migration of the actual material organ from somite to somite, but by translation of the quality or morphogenetic peculiarity from somite to somite accompanied by correlative change in all the somites of the series. The phenomenon may be compared to the transposition of a piece of music to a higher or lower key. It is thus that the lateral fins of fishes move up and down the scale of vertebral somites ;¹ and thus that whole regions (tagmata), such as those indicated

¹ Except in such cases as have just been cited.—E. R. L., 1904.

by the names cervical, thoracic, lumbar, and sacral, are translated (accompanied by terminal increase or decrease in the total number of somites) so as to occupy differing numerical positions in closely allied forms (cf. the varying number of cervical somites in allied reptiles and birds).

What, in this rapid enumeration, we will venture to call the EIGHTH LAW of metamerism is the law of homœosis, as it is termed by Bateson (1). Homœosis is the making of a merome into the likeness of one belonging to another metamere, and is the opposite of the process of "heterosis"—already mentioned. We cite this law here because the result of its operation is to simulate the occurrence of dislocation of meromes, and has to be carefully distinguished from that process. A merome can and does, in individual cases of abnormality, assume the form and character of the corresponding merome of a distant somite. Thus the antenna of an insect has been found to be replaced by a perfectly well-formed walking leg. After destruction of the eye-stalk of a shrimp a new growth appears, having the form of an antenna. Other cases are frequent in Crustacea as individual abnormalities. They prove the existence in the mechanism of metamerised animals of structural conditions which are capable of giving these results. What those structural conditions are is a matter for separate inquiry, which we cannot even touch here. It is not improbable that homœosis of distant meromes may have given rise to permanent structural changes characteristic of whole groups of Arthropoda, supposing the abnormality once established to be favoured by natural selection. Possibly the chelate condition of the præoral appendages of Arachnida may be due to homœosis transferring the chelate form of post-oral limbs to what were previously antenniform rami.

We now come to the question of the production of new somites or the addition of new somites to the series, and the converse problem of the suppression of somites, whole or partial. We state as the NINTH LAW of metamerism "that new somites or metameres are added to a chain consisting of

two or more somites by growth and gradual elaboration—what is called “budding”—of the anterior border of the hindermost somite. This hindermost somite is therefore different from all the other somites, and is called the ‘telson.’ However long or short or heteromerised the chain may be, new metameres or somites are only produced at the anterior border of the telson, except in the Vertebrata.” That is the general law; but amongst some groups of metamerised animals partial exceptions to it occur. It is probably absolutely true for the Arthropoda from lowest to highest. It is not so certain that it is true for the Chaetopoda, and would need modification in statement to meet the cases of fissiparous multiplication occurring among Syllids and Naidids. In the Vertebrata, where tagmosis and heterosis of meromes and dislocation of meromes and tagmata are, so to speak, rampant, new formation of metameres (at any rate as represented by important meromes) takes place at more than one point in the chain. Such points are found where two highly diverse “tagmata” abut on one another. It is possible, though the evidence at present is entirely against the supposition, that at such points in Arthropoda new somites may be formed.¹ Such new somites are said to be “intercalated.” The question of the intercalation of vertebræ in the Vertebrata has received some attention. It must be remembered that a vertebra, even taken with its muscular, vascular, and neural accessories, is only a partial metamere—a merome, and that, so far as complete metameres are concerned, the

¹ The curious case of superabundant parapodia in the hinder somites of *Apus* has already been cited and referred to as an example of autorhythmic multiplication of meromes. There is some reason for regarding the extra pairs of legs as being “intercalated” after the formation of the somite as a single unit or merome by growth from the telson. Supposing, as appears to be the case, that as the *Apus* increases in size, the number of extra pairs of legs on a non-terminal somite increases, these added meromes are certainly intercalated, and represent incomplete intercalated metameres. The intercalation of new elements does not really go much further than this in Vertebrata, for a vertebra with its myoskeletal tissues is only a merome, and not a complete metamere.

Vertebrata do conform to the same law as the Arthropods. Intercalation of meromes—branchial, vertebral, and dermal (fin-supports)—seems to have taken place in Vertebrata in the fishes, while in higher groups intercalation of vertebræ in large series has been accepted as the only possible explanation of the structural facts established by the comparison of allied groups. The elucidation of this matter forms a very important part of the work lying to the hand of the investigator of vertebrate anatomy, and it is possible that the application of Goodrich's law (the seventh of our list) may throw new light on the matter.

In regard to the diminution in the number of somites in the course of the historical development of those various groups of metamerised animals, which have undoubtedly sprung from ancestors with more numerous somites than they themselves possess, it appears that we may formulate the following laws as the tenth, eleventh, twelfth, and thirteenth laws of metamerism.

The TENTH LAW is that individual somites tend to atrophy and finally disappear as distinct structures, most readily at the anterior and the posterior ends of the series constituting an animal body. This is very generally exhibited in the head of Arthropoda, where, however, the operation of the law is largely modified by fusion (see below). With regard to the posterior end of the body, the atrophy of segments does not, as a rule, affect the telson itself so much as the somites in front of it and its power of producing new somites. Sometimes, however, the telson is very minute and non-chitinated (Hexapoda).

The ELEVENTH LAW may be stated thus:—Any somite in the series which is the anterior or posterior somite of a tagma may become atrophied, reduced in size, or partially aborted by the suppression of some of its meromes; and finally, such a somite may disappear and leave no obvious trace in the adult structure of its presence in ancestral forms. This is called the excalation of a somite. Frequently, however, such "excalated" somites are obvious in the embryo or leave some

merome (e. g. neuromere, muscle, or chitin-plate) which can be detected by minute observation (microscopic) as evidence of their former existence. The somite of the maxillipede (third post-oral appendage) of *Apus cancriformis* is a good example of a somite on its way to excalation. The third præ-oral and the præmaxillary somites of Hexapod insects are instances where the only traces of the vanished somite are furnished by the microscopic study of early embryos. The prægenital somite of the Arachnida is an example of a somite which is preserved in some members of the group and partially or entirely excalated in other cases, sometimes with fusion of its remnants to neighbouring somites.

The TWELFTH LAW of metamerism might very well be placed in logical order as the first. It is the law of lipomerism, and asserts that just as the metameric condition is produced by a change in the bodies of the descendants of unisegmental ancestors, so highly metamerised forms, i. e. strongly segmented forms with specialised regions of differentiated metameres, may gradually lose their metamerised structure and become apparently and practically unisegmental animals. The change here contemplated is not the atrophy of terminal segments one by one so as to reduce the size of the animal and leave it finally as a single somite. On the contrary, no loss of size or of high organisation is necessary. But one by one, and gradually, the metameric grouping of the bodily structures disappears. The cuticle ceases to be thickened in rings; the muscles of the body-wall overrun their somite boundaries. Internal septa disappear. The nerve-ganglia concentrate or else become diffused equally along the cords; one pair of renal cœlomoducts and one pair of genital cœlomoducts grow to large size and remain—the rest disappear. The appendages atrophy or become limited to one or two pairs, which are widely dislocated from their ancestral position. The animal ceases to present any indication of metameric repetition of parts in its entire structure. Degrees in this process are frequently to be recognised. We certainly can observe such a change in the posterior region

of some Arthropods, such as the hermit crabs and the spiders. Admitting that the Echiurids are descended from Chaetopoda, such a change has taken place in them amounting to little short of complete lipomerism, though not absolutely complete.

Recent suggestions as to the origin of the Mollusca involve the supposition that such an effacement of once well-marked metamerism has occurred in them, leaving its traces only in a few structures such as the multiple gill-plumes and shell-shields of the Chitons and the duplicated renal sacs of Nautilus.

A further matter of importance in this connection is that when the old metameres have been effaced a new secondary segmentation may arise, as in the jointed worm-like body of the degenerate *Acarus*, *Demodex folliculorum*.

Such secondary annulation of the soft body calls to mind the secondary annulation of the metameres of leeches and some earthworms. Space does not permit of more than an allusion to this subject, but it is worth while noting that the secondary annuli marking the somites of leeches and Lumbricidæ in definite number and character are perhaps comparable to the redundant pairs of appendages on the hinder somites of *Apus*, and are in both cases examples of independent repetition of tegumentary meromes—a sort of ineffectual attempt to subdivide the somite which only prevails on the more readily susceptible meromes of the integument.

The development of secondary metameric annulations within the area of a complete somite is not recorded among Arthropoda. It deserves distinct recognition as “hypometamerism” or formation of “somatidia.”

The last law of metamerism which we shall attempt to formulate here, as the THIRTEENTH, relates to the fusion or blending of neighbouring somites. There are, without doubt, a large number of important generalisations to be arrived at hereafter from the further study of the metamerism of Vertebrata and the peculiar phenomena exhibited by the dislocated meromes of the vertebrate’s somites. But this is

not the place in which to attempt an outline of the special laws of vertebrate metamerism. Fusion of adjacent somites has often been erroneously interpreted in the study of Arthropoda. There are, in fact, very varying degrees of fusion which need to be carefully distinguished. The following generalisation may be formulated :—"The homologous meromes of two or more adjacent somites tend to fuse with one another by a blending of their substance. Very generally, but not invariably, the fused meromes are found as distinct separated structures in the embryo of the animal in which they unite at a later stage of growth." The fusion of neighbouring meromes is often preceded by more or less extensive atrophy of the somites concerned, and by arrest of development in the individual ontogeny. Thus a case of fusion of partially atrophied somites may simulate the appearance of incipient merogenesis or formation of new somites; and vice versâ, incipient merogenesis may be misinterpreted as a case of fusion of once separate and fully formed somites. Moreover the two phenomena, merogenesis and fusion of meromes, actually occur side by side in some cases, as in the pygidial shields of the Trilobitæ and *Limulus*.

The most commonly noted cases of fusion of metameres are simply cases of the fusion of the tegumentary meromes—usually the terga only. Such a fusion has really no very serious morphological importance: it is superficial and readily acquired. It amounts to no more than the disposition of chitinous cuticle of equal thickness over the area of the terga of the somites concerned instead of the thinning of the cuticular deposit at the adjacent borders of the somites. The somites consequently lose their hinge; they can no longer be flexed one on the other. Atrophy of the muscles related to such flexure necessarily follows. The mesosomatic portion of the posterior carapace of *Limulus* is no more than such a superficial fusion: the other meromes of the ankylosed somites (appendages, neuromeres, blood-vessels, etc.) are unaffected. Such, too, is the case with the pygidial

shields of many Trilobites. On the other hand, the telson, which is joined in both these cases with the superficially fused segments by a fusion of its chitinous cuticle with that of its last-formed or budded somite, can only take part in the fusion as a result of arrest in its activity, which amounts to a late supervening atrophy. This arrest of the telson's special bud growth may take place very early, in which case we get a large telsonic shield and only a very few somites in front of it—none soldered to the telson as in *Agnostus* and *Ilenus*; or it may take place later when eight post-cephalic (opisthosomatic) somites have been formed as in *Limulus*—the last two incompletely. Or, again, thirty or more somites may have been produced before the arrest takes place, and fifteen of these may be ankylosed with the telson to form the pygidial shield (*Phacops*, etc.).

A more complete fusion of somites is that seen in the head of Arthropoda. The head or prosoma of Arthropoda is a tagma consisting of one, two, or three prosthomeres or somites in front of the mouth, and of one, two, three, up to five or six opisthomeres. The cephalic tagma or prosoma may thus be more or less sharply divided into two sub-tagmata, the præ-oral and the post-oral.

The shifting of the mouth backwards in Arthropoda so as to allow segments which once were post-oral to take up a præoral position, as prosthomeres, must be regarded as a case of dislocation of the meromes concerned (sixth law), like the forward travelling of a fish's pelvic fins. The anus does not appear to be liable to such dislocation in Arthropoda, but it certainly does travel away from its parental metamere in the Vertebrata, and may possibly do so in Chaetopoda when what must be called "lipomerism" or general obliteration of a metameric ordering of parts sets in. Such "lipomerism" must be supposed to have affected the Chaetopod ancestors of the Sipunculids, if those latter worms are to be traced genetically to the former, and the anus has shifted to the anterior third of the body. However that may be, the conception (first put forward by Lankester in 1875)

(2) of the backward movement of the mouth in Arthropoda from the first somite to the second, third, or even fourth in the original post-oral series, is not only justified by embryological observation of the shifting in question, but finds its parallel in other instances of the law of dislocation of meromes.

The fusion of the cephalic or prosomatic somites not only extends to tegumentary structures, but to muscles, blood-vessels, and markedly to neuromeres. However, in the embryo of many Arthropoda the original neuromeres of the præoral somites can be distinguished, and in many cases the coelomic cavities. Also it is a noteworthy fact that the tegumentary fusion (cephalic carapace, prosomatic carapace) appears sometimes to break down secondarily (e.g. *Squilla* among Crustacea and *Galeodes* and *Tarassidæ* among Arachnida). It appears that we must recognise as a principle that such fusions as the carapaces of Arthropoda can revert to the condition of free movable plates; and therefore we must not assume that forms with fused tergal plates are necessarily later, genetically, than allied forms with free movable tergal plates.

When such reversion to a movable series of dorsal plates occurs it must not be assumed that any corresponding change takes place in the deeper meromes. On the whole, fusion and ankylosis of somites is not in itself necessarily a deep-seated or far-reaching process. It may or may not be accompanied by dislocation of important meromes or by lipomerism; whilst,—as for instance in the opisthosoma of the spiders, opiliones, and acari—dislocation and lipomerism may occur without fusion of tegumentary plates, and with, on the contrary, a dwindling and eventual atrophy of such plates.

The general considerations as to metamerism set forth above will enable us to proceed to a consideration of the characters which distinguish the various groups of Arthropoda, and to justify the classification with which we started.

The Theory of the Arthropod Head.—The arthropod

head is a tagma or group of somites which differ in number and in their relative position in regard to the mouth, in different classes. In a simple Chætopod (fig. 1) the head consists of the first somite only; that somite is perforated by the mouth, and is provided with a prostomium or præoral lobe. The prostomium is essentially a part or outgrowth of the first somite, and cannot be regarded as itself a somite. It gives rise to a nerve-ganglion mass, the prostomial ganglion. In the marine Chætopods (the Polychæta) (fig. 2) we find

FIG. 1.

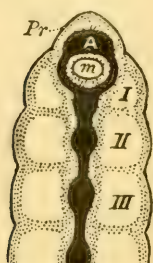


FIG. 2.

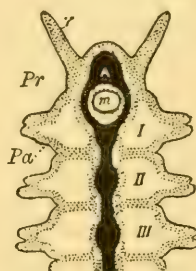


FIG. 1.—Diagram of the head and adjacent region of an Oligochaete Chætopod. *Pr*, the prostomium; *m*, the mouth; *A*, the prostomial ganglion-mass or archicerebrum; *I*, *II*, *III*, cœlom of the first, second, and third somites. (From Goodrich, 'Q. J. Micr. Sci.,' vol. xl, p. 247.)

FIG. 2.—Diagram of the head and adjacent region of a Polychæte Chætopod. Letters as in Fig. 1, with the addition of *T*, prostomial tentacle; *Pa*, parapodium. (From Goodrich.)

the same essential structure, but the prostomium may give rise to two or more tactile tentacles, and to the vesicular eyes. The somites have well-marked parapodia, and the second and third, as well as the first, may give rise to tentacles which are directed forward, and thus contribute to form "the head." But the mouth remains as an inpushing of the wall of the first somite.

The Arthropoda are all distinguished from the Chætopoda by the fact that the head consists of one or more somites which lie in front of the mouth (now called prothomeres),

as well as of one or more somites behind it (opisthomeres). The first of the post-oral somites invariably has its parapodia modified so as to form a pair of hemignaths (mandibles). Twenty-five years ago the question arose as to whether the somites in front of the mouth are to be considered as derived from the prostomium of a Chætopod-like ancestor. Milne-Edwards and Huxley had satisfied themselves with discussing and establishing, according to the data at their command, the number of somites in the Arthropod head, but had not considered the question of the nature of the præoral somites. Lankester (2) was the first to suggest that (as is actually the fact in the Nauplius larva of Crustacea) the præoral somites or prosthomeres and their appendages were ancestrally post-oral, but have become præoral "by adaptational shifting of the oral aperture." This has proved to be a sound hypothesis, and is now accepted as the basis upon which the Arthropod head must be interpreted (see Korschelt and Heider [3]). Further, the morphologists of the 'fifties appear, with few exceptions, to have accepted a preliminary scheme with regard to the Arthropod head and Arthropod segmentation generally, which was misleading and caused them to adopt forced conclusions and interpretations. It was conceived by Huxley, among others, that the same number of cephalic somites would be found to be characteristic of all the diverse classes of Arthropoda, and that the somites not only of the head, but of the various regions of the body, could be closely compared in their numerical sequence in classes so distinct as the Hexapods, Crustaceans, and Arachnids.

The view which it now appears necessary to take is, on the contrary, this—viz. that all the Arthropoda are to be traced to a common ancestor resembling a Chætopod worm, but differing from it in having lost its chætæ and in having a prosthomere in front of the mouth (instead of prostomium only) and a pair of hemignaths (mandibles) on the parapodia of the buccal somite. From this ancestor Arthropods with heads of varying degrees of complexity have been developed

characteristic of the different classes, whilst the parapodia and somites of the body have become variously modified and grouped in these different classes. The resemblances which the members of one class often present to the members of another class in regard to the form of the limb-branches (rami) of the parapodia, and the formation of tagmata (regions) are not hastily to be ascribed to common inheritance, but we must consider whether they are not due to homoplasy—that is, to the moulding of natural selection acting in the different classes upon fairly similar elements under like exigencies.

The structure of the head in Arthropods presents three profoundly separated grades of structure dependent upon the number of prosthomeres which have been assimilated by the præoral region. The classes presenting these distinct plans of head-structure cannot be closely associated in any scheme of classification professing to be natural. *Peripatus*, the type genus of the class Onychophora, stands at the base of the series with only a single prosthomere (fig. 3). In *Peripatus* the prostomium of the Chaetopod-like ancestor is atrophied, but it is possible that two processes on the front of the head (FP) represent in the embryo the dwindled prostomial tentacles. The single prosthomere carries the retractile tentacles as its "parapodia." The second somite is the buccal somite (II, fig. 3); its parapodia have horny jaws on their ends, like the claws on the following legs (fig. 8), and act as hemignaths (mandibles). The study of sections of the embryo establishes these facts beyond doubt. It also shows us that the neuromeres, no less than the embryonic coelomic cavities, point to the existence of one, and only one, prosthomere in *Peripatus*, of which the "Protocerebrum," P, is the neuromere, whilst the Deutocerebrum, D, is the neuromere of the second or buccal somite. A brief indication of these facts is given by saying that the Onychophora are "deutero-gnathous,"—that is to say, that the buccal somite carrying the mandibular hemignaths is the second of the whole series.

What has become of the nerve-ganglion of the prostomial lobe of the Chætopod in *Peripatus* is not clearly ascertained, nor is its fate indicated by the study of the embryonic head of other Arthropods so far. Probably it is fused with the protocerebrum, and may also be concerned in the history of the very peculiar paired eyes of *Peripatus*, which are like those of Chætopods in structure—viz. vesicles with an intra-

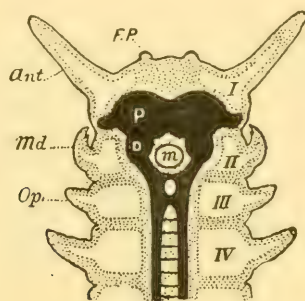


FIG. 3.—Diagram of the head and adjacent region of *Peripatus*. Monoprosthomerous. *m*, Mouth; *I*, coelom of the first somite which carries the antennæ, and is in front of the mouth; *II*, coelom of the second somite, which carries the mandibles (hence deutero-gnathous); *III* and *IV*, coelom of the third and fourth somites; *F.P.*, rudimentary frontal processes, perhaps representing the prostomial tentacles of Polychæta; *Ant.*, antenna or tactile tentacle; *MD*, mandible; *Op.*, oral papilla; *P*, protocerebrum or foremost cerebral mass belonging to the first somite; *D*, deutocerebrum, consisting of ganglion cells belonging to the second or mandibular somite. (After Goodrich.)

vesicular lens, whereas the eyes of all other Arthropods have essentially another structure, being “cups” of the epidermis, in which a knob-like or rod-like thickening of the cuticle is fitted as refractive medium.

In Diplopoda (*Julus*, etc.) the results of embryological study point to a composition of the front part of the head exactly similar to that which we find in Onychophora. They are deutero-gnathous.

The Arachnida present the first stage of progress. Here embryology shows that there are two prosthomeres (fig. 4),

and that the gnathobases of the chelæ which act as the first pair of hemignaths, are carried by the third somite. The Arachnida are therefore tritognathous. The two prosthomerites are indicated by their cœlomic cavities in the embryo (I and II, fig. 4), and by two neuromeres, the protocerebrum and the deutocerebrum. The appendages of the first prosthomere are not present as tentacles, as in *Peripatus* and *Diplopods*, but are possibly represented by the eyes or possibly altogether aborted. The appendages of the second prosthomere are the well-known chelicerae of the Arachnids, rarely,

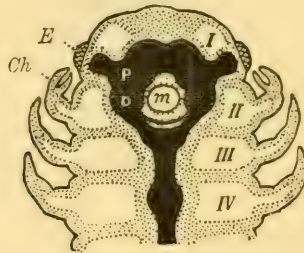


FIG. 4.—Diagram of the head and adjacent region of an Arachnid. Diprosthomerous in the adult condition, though embryologically the appendages of somite *II* and the somite itself are, as here drawn, not actually in front of the mouth. *E*, lateral eye; *Ch*, chelicera; *m*, mouth; *P*, protocerebrum; *D*, deutocerebrum; *I*, *II*, *III*, *IV*, cœlom of the first, second, third, and fourth somites. (After Goodrich.)

if ever, anteuiform, but modified as “retroverts” or clasp-knife fangs in spiders.

The Crustacea (fig. 5) and the Hexapoda (fig. 6) agree in having three somites in front of the mouth, and it is probable, though not ascertained, that the Chilopoda (*Scolopendra*, etc.) are in the same case. The three prosthomerites or præoral somites of Crustacea due to the sinking back of the mouth one somite farther than in Arachnida are not clearly indicated by cœlomic cavities in the embryo, but their existence is clearly established by the development and position of the appendages and by the neuromeres.

The eyes in some Crustacea are mounted on articulated stalks, and from the fact that they can after injury be replaced by antenna-like appendages it is inferred that they represent the parapodia of the most anterior prosthomere. The second prosthomere carries the first pair of antennæ and

FIG. 5.

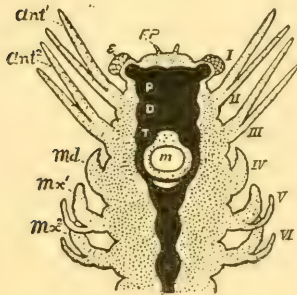


FIG. 6.

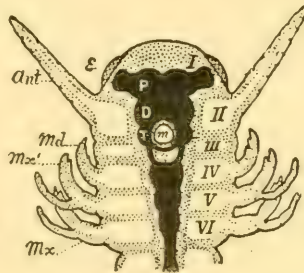


FIG. 5.—Diagram of the head of a crustacean. Triprosthomerous. F. P, frontal processes (observed in Cirrhiped nauplius-larvæ), probably representing the prostomial tentacles of Chætopods; *e*, eye; *Ant*¹, first pair of antennæ; *Ant*², second pair of antennæ; *md*, mandible; *mx*¹, *mx*², first and second pairs of maxillæ; *m*, mouth; *I*, *II*, *III*, the three prosthomeres; *IV*, *V*, *VI*, the three somites following the mouth; *P*, protocerebrum; *D*, deutocerebrum; *T*, tritocerebrum. (After Goodrich.)

FIG. 6.—Diagram of the head of a Hexapod insect. *e*, eye; *ant*, antenna; *md*, mandible; *mx*¹, first maxilla; *mx*², second maxilla; *m*, mouth; *I*, region of the first or eye-bearing prosthomere; *II*, cœlom of the second antenna-bearing prosthomere; *III*, cœlom of the third prosthomere devoid of appendages; *IV*, *V*, and *VI*, cœlom of the fourth, fifth, and sixth somites; *P*, protocerebrum belonging to the first prosthomere; *D*, deutocerebrum belonging to the second prosthomere; *T*, tritocerebrum belonging to the third prosthomere. (After Goodrich.)

the third the second pair of antennæ. Sometimes this pair of appendages has not a merely tactile jointed ramus, but is converted into a claw or clasper. Three neuromeres—a proto-, deutero-, and tritocerebrum—corresponding to those three prosthomeres, are sharply marked in the embryo. The fourth somite is that in which the mouth now opens, and which accordingly has its appendages converted into

hemignathous mandibles. The Crustacea are tetartognathous.

The history of the development of the head has been carefully worked out in the Hexapod insects. As in Crustacea and Arachnida, a first prosthomere is indicated by the paired eyes and the protocerebrum; the second prosthomere has a well-marked cœlomic cavity, carries the antennæ, and has the deuterocerebrum for its neuromere. The third prosthomere is represented by a well-marked pair of cœlomic cavities and the tritocerebrum (III, fig. 6), but has no appendages. They appear to have aborted. The existence of this third prosthomere, corresponding to the third prosthomere of the Crustacea, is a strong argument for the derivation of the Hexapoda, and with them the Chilopoda, from some offshoot of the Crustacean stem or class. The buccal somite, with its mandibles, is in Hexapoda, as in Crustacea, the fourth: they are tetartognathous.

The adhesion of a greater or less number of somites to the buccal somite posteriorly (opisthomeres) is a matter of importance, but of minor importance, in the theory and history of the Arthropod head. In *Peripatus* no such adhesion or fusion occurs. In *Diplopoda* two opisthomeres—that is to say, one in addition to the buccal somite—are united by a fusion of their terga with the terga of the prosthomeres. Their appendages are respectively the mandibles and the gnathochilarium.

In *Arachnida* the highest forms exhibit a fusion of the tergites of five post-oral somites to form one continuous carapace united with the terga of the two prosthomeres. The five pairs of appendages of the post-oral somites of the head or prosoma thus constituted all primitively carry gnathobasic projections on their coxal joints, which act as hemignaths; in the more specialised forms the mandibular gnathobases cease to develop.

In Crustacea the fourth or mandibular somite never has less than the two following somites associated with it by the adaptation of their appendages as jaws, and the ankylosis of

their terga with that of the prosthomeres. But in higher Crustacea the cephalic "tagma" is extended, and more somites are added to the fusion, and their appendages adapted as jaws of a kind.

The Hexapoda are not known to us in their earlier or more primitive manifestations; we only know them as possessed of a definite number of somites arranged in definite numbers in three great tagmata. The head shows two jaw-bearing somites besides the mandibular somite (V, VI, in fig. 6)—thus six in all (as in some Crustacea), including prosthomeres, all ankylosed by their terga to form a cephalic shield. There is, however, good embryological evidence in some Hexapods of the existence of a seventh somite, the supra-lingual, occurring between the somite of the mandibles and the somite of the first maxillæ (4). This segment is indicated embryologically by its paired coelomic cavities. It is practically an excalated somite, having no existence in the adult. It is probably not a mere coincidence that the Hexapod, with its two rudimentary somites devoid of appendages, is thus found to possess twenty-one somites, including that which carries the anus, and that this is also the number present in the Malacostracous Crustacea.

The Segmental Lateral Appendages or Limbs of Arthropoda.—It has taken some time to obtain any general acceptance of the view that the parapodia of the Chaetopoda and the limbs of Arthropoda are genetically identical structures; yet if we compare the parapodium of *Tomopteris* or of *Phyllodoce* with one of the foliaceous limbs of *Branchipus* or *Apus* the correspondences of the two are striking. An erroneous view of the fundamental morphology of the crustacean limb, and consequently of that of other Arthropoda, came into favour owing to the acceptance of the highly modified limbs of *Astacus* as typical. Protopodite, endopodite, exopodite, and epipodite were considered to be the morphological units of the crustacean limb. Lankester (5) has shown (and his views have been accepted by Professors Korschelt and Heider in their treatise on 'Embryology')

that the limb of the lowest Crustacea, such as *Apus*, consists of a corm or axis which may be jointed, and gives rise to out-

FIG. 7.

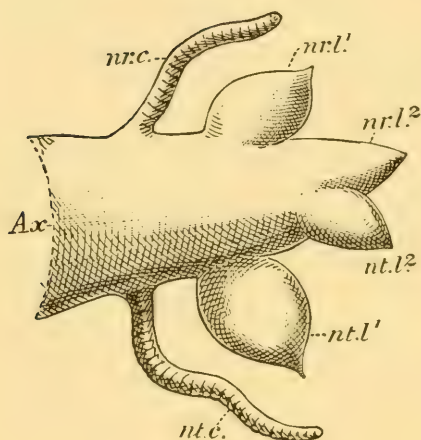


FIG. 8.

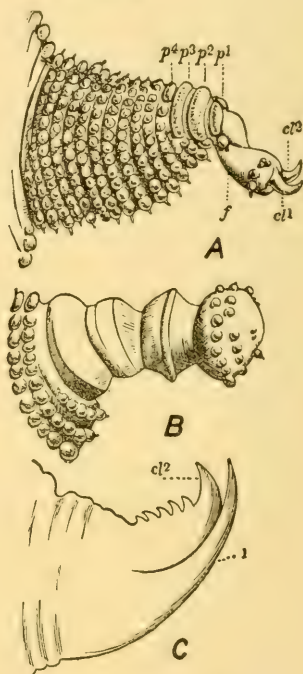


FIG. 7.—Diagram of the somite-appendage or parapodium of a Polychæte Chaetopod. The chaetæ are omitted. *Ax*, the axis; *nr. c.*, neuropodial cirrhus; *nr. l¹*, *nr. l²*, neuropodial lobes or endites; *nt. c.*, notopodial cirrhus; *nt. l¹*, *nt. l²*, notopodial lobes or exites. The parapodium is represented with its neural or ventral surface uppermost. (Original.)

FIG. 8.—Three somite-appendages or parapodia of *Peripatus*. *A*, a walking leg; *p* to *p⁴*, the characteristic "pads;" *f*, the foot; *cl¹*, *cl²*, the two claws; *B*, an oral papilla, one of the second pair of post-oral appendages; *C*, one of the first post-oral pair of appendages or mandibles; *cl¹*, *cl²*, the greatly enlarged claws. (Compare *A*.)

The appendages are represented with the neural or ventral surface uppermost. (Original.)

growths, either leaf-like or filiform, on its inner and outer margins (endites and exites). Such a corm (see figs. 9 and 10), with its outgrowths, may be compared to the simple

parapodia of Chaetopoda with cirrhi and branchial lobe (fig. 7). It is by the specialisation of two "endites" that the endopodite and exopodite of higher Crustacea are formed, whilst a flabelliform exite is the homogen or genetic equivalent of the epipodite (see Lankester, "Observations and Reflections on *Apus canceriformis*," 'Q. J. Micr. Sci.'). The reduction of the outgrowth-bearing "corm" of the parapodium of either a Chaetopod or an Arthropod to a simple cylindrical stump, devoid of outgrowths, is brought about

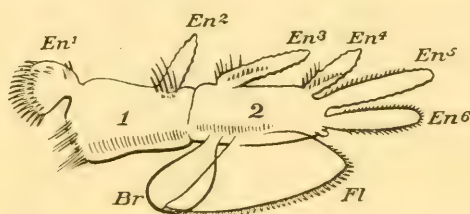


FIG. 9.—The second thoracic (fifth post-oral) appendage of the left side of *Apus canceriformis*, placed with its ventral or neural surface uppermost to compare with Figs. 7 and 8. 1, 2, the two segments of the axis; *en¹*, the gnathobase; *en²* to *en⁶*, the five following "endites;" *fl*, the flabellum or anterior exite; *br*, the bract or posterior exite. (After Lankester, 'Q. J. Micr. Sci.,' vol. xxi, 1881.)

when mechanical conditions favour such a shape. We see it in certain Chaetopods (e.g. *Hesione*) and in the Arthropod *Peripatus* (fig. 8). The conversion of the Arthropod's limb into a jaw, as a rule, is effected by the development of an endite near its base into a hard, chitinated, and often toothed gnathobase (see figs. 9 and 10, *en¹*). It is not true that all the biting processes of the Arthropod limb are thus produced, —for instance, the jaws of *Peripatus* are formed by the axis or corm itself; whilst the poison-jaws of Chilopods, as also their maxillæ, appear to be formed rather by the apex or terminal region of the ramus of the limb; but the opposing jaws (= hemignaths) of Crustacea, Arachnida, and Hexapoda are gnathobases, and not the axis or corm. The endopodite (corresponding to the fifth endite of the limb of *Apus*, see fig. 9) becomes in Crustacea the "walking leg" of the mid-

region of the body ; it becomes the palp or jointed process of anterior segments. A second ramus, the "exopodite," often is also retained in the form of a palp or feeler. In *Apus*, as

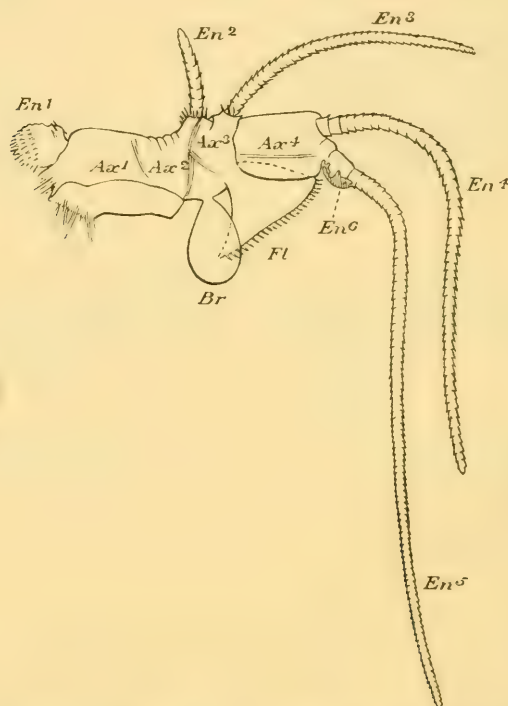


FIG. 10.—The first thoracic (fourth post-oral) appendage of *Apus cancriformis* (right side). Ax^1 to Ax^4 , the four segments of the axis with muscular bands; En^1 , gnathobase; En^2 to En^5 , the elongated jointed endites (rami); En^6 , the rudimentary sixth endite (exopodite of higher Crustacea); Fl , the flabellum which becomes the epipodite of higher forms; Br , the bract devoid of muscles and respiratory in function. (After Lankester, 'Q. J. Micr. Sci.,' vol. xxi, 1881.)¹

the figure shows, there are four of these "antenna-like" palps or filaments on the first thoracic limb. A common modification of the chief ramus of the Arthropod parapodium is the chela or nipper formed by the elongation of the pen-

¹ This figure has been re-drawn for the present reprint.—E. R. L.

ultimate joint of the ramus, so that the last joint works on it—as, for instance, in the lobster's claw. Such chelate rami or limb-branches are independently developed in Crustacea and in Arachnida, and are carried by somites of the body

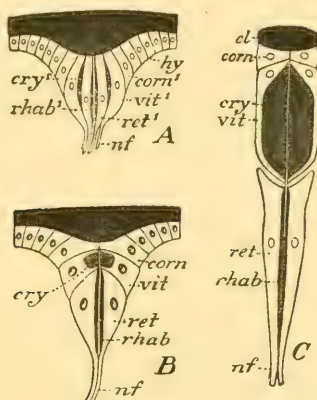


FIG. 11.—Diagram to show the derivation of the unit or "ommatidium" of the compound eye of Crustacea and Hexapoda, *C*, from a simple monostichous monostichous eye resembling the lateral eye of a scorpion, *A*, or the unit of the compound lateral eye of *Limulus* (see article ARACHNIDA, Figs. 22 and 23). *B* represents an intermediate hypothetical form in which the cells beneath the lens are beginning to be superimposed as corneagen, vitrella, and retinula, instead of standing side by side in horizontal series. The black represents the cuticular product of the epidermal cells of the ocular area, taking the form either of lens, *cl*, of crystalline body, *cry*, or of rhabdom, *rhab*; *hy*, hypodermis or epidermal cells; *corn*, laterally placed cells in the simpler stage *A*, which like the nerve-end cells, *vit*¹ and *ret*¹, are corneagens or lens-producing; *corn*, specialised corneagen or lens-producing cells; *vit*¹, potential vitrella cells with *cry*, potential crystalline body now indistinguishable from retinula cells and rhabdomeres; *vit*, vitrella cell with *cry*, its contained cuticular product, the crystalline cone or body; *vit*¹, *rhab*¹, retinula cells and rhabdom of scorpion undifferentiated from adjacent cells, *vit*¹; *ret*¹, retinula cell; *rhab*, rhabdom; *nf*, optic nerve-fibres. (Modified from Watasse.)

which do not correspond in position in the two groups. The range of modification of which the rami or limb-branches of the limbs of Arthropoda are capable is very large, and in allied orders, or even families or genera, we often find what is certainly the palp of the same appendage (as determined

by numerical position of the segments)—in one case antenniform, in another chelate, in another pediform, and in another reduced to a mere stump or absent altogether. Very probably the power which the appendage of a given segment has of assuming the perfected form and proportions previously attained by the appendage of another segment must be classed as an instance of "homœosis," not only where such a change is obviously due to abnormal development or injury, but also where it constitutes a difference permanently established between allied orders or smaller groups, or between the two sexes.

The most extreme disguise assumed by the Arthropod parapodium or appendage is that of becoming a mere stalk supporting an eye, a fact which did not obtain general credence until the experiments of Herbst, in 1895, who found, on cutting off the eye-stalk of *Palæmon*, that a jointed antenna-like appendage was regenerated in its place. Since the eye-stalks of *Podothalmate* Crustacea represent appendages, we are forced to the conclusion that the sessile eyes of other Crustacea, and of other Arthropoda generally, indicate the position of appendages which have atrophied.¹

From what has been said it is apparent that we cannot, in attempting to discover the affinities and divergences of the various forms of Arthropoda, attach a very high phylogenetic value to the coincidence or divergence in form of the appendages belonging to the somites compared with one another.

The principal forms assumed by the Arthropod parapodium and its rami may be thus enumerated :

(1) Axial corm well developed, unsegmented or with two to four segments ; lateral endites and exites (rami) numerous and of various lengths (certain limbs of lower Crustacea).

(2) Corm, with short, unsegmented rami, forming a flat-

¹ H. Milne-Edwards, who was followed by Huxley, long ago formulated the conclusion that the eye-stalks of Crustacea are modified appendages, basing his argument on a specimen of *Palinurus* (figured in Bateson's book) (1), in which the eye-stalk of one side is replaced by an antenniform palp. Hofer (6) in 1894 described a similar case in *Astacus*.

tened foliaceous appendage, adapted to swimming and respiration (trunk limbs of Phyllopods).

(3) Corm alone developed, with no endites or exites, but provided with terminal chitinous claws (ordinary leg of *Peripatus*), with terminal jaw teeth (jaw of *Peripatus*), or with blunt extremity (oral papilla of same) (see fig. 8).

(4) Three of the rami of the primitive limb (endites 5 and 6 and exite 1) specially developed as endopodite, exopodite, and epipodite, the first two often as firm and strongly chitinised, segmented, leg-like structures; the original axis or corm reduced to a basal piece, with or without a distinct gnathobase (endite 1), typical triramose limb of higher Crustacea.

(5) One ramus (the endopodite) alone developed—the original axis or corm serving as its basal joint with or without gnathobase. This is the usual uniramous limb found in the various classes of Arthropoda. It varies as to the presence or absence of the jaw process and as to the stoutness of the segments of the ramus, their number (frequently six, plus the basal corm), and the modification of the free end. This may be filiform, or brush-like, or lamellate when it is an antenna or palp; a simple spike (walking leg of Crustacea, of other aquatic forms, and of Chilopods and Diplopods); the terminal joint flattened (swimming leg of Crustacea and Gigantostrea); the terminal joint provided with two or with three recurved claws (walking leg of many terrestrial forms—e.g. Hexapoda and Arachnida); the penultimate joint with a process equal in length to the last joint, so as to form a nipping organ (chelæ of Crustaceans and Arachnids); the last joint reflected and movable on the penultimate, as the blade of a clasp-knife on its handle (the retrovert, toothed so as to act as a biting jaw in the Hexapod Mantis, the Crustacean *Squilla*, and others; with the last joint produced into a needle-like stabbing process in spiders).

(6) Two rami developed (usually, but perhaps not always, the equivalents of the endopodite and exopodite) supported on the somewhat elongated corm (basal segment). This is

the typical "biramose limb" often found in Crustacea. The rami may be flattened for swimming, when it is "a biramose swimmeret," or both or only one may be filiform and finely annulate; this is the form often presented by the antennæ of Crustacea, and rarely by præoral appendages in other Arthropods.

(7) The endopoditic ramus is greatly enlarged and flattened, without or with only one jointing, the corm (basal segment) is evanescent; often the plate-like endopodites of a pair of such appendages unite in the middle line with one another or by the intermediary of a sternal upgrowth and form a single broad plate. (These are the plate-like swimmerets and opercula of Gigantostroma and Limulus among Arachnids and of Isopod crustaceans. They may have rudimentary exopodites, and may or may not have branchial filaments or lamellæ developed on their posterior faces. The simplest form to which they may be reduced is seen in the genital operculum of the scorpion.)

(8) The gnathobase becomes greatly enlarged and not separated by a joint from the corm; it acts as a hemignath or half-jaw working against its fellow of the opposite side. The endopodite may be retained as a small segmented palp at the side of the gnathobase or disappear (mandible of Crustacea, Chilopoda, and Hexapoda).

(9) The corm becomes the seat of a development of a special visual organ, the Arthropod eye (as opposed to the Chætopod eye). Its jointing (segmentation) may be retained, but its rami disappear (podophthalmous Crustacea). Usually it becomes atrophied, leaving the eye as a sessile organ upon the præoral region of the body. (The eye-stalk and sessile lateral eyes of Arthropoda generally, exclusive of Peripatus.)

(10) The forms assumed by special modification of the elements of the parapodium in the maxillæ, labium, etc., of Hexapods, Chilopods, Diplopods, and of various Crustacea deserve special enumeration, but cannot be dealt with without ample space and illustration.

It may be pointed out that the most radical difference presented in this list is that between appendages consisting of the corm alone without rami (*Onychophora*) and those with more or less developed rami (the rest of the *Arthropoda*). In the latter class we should distinguish three phases: (*a*) those with numerous and comparatively undeveloped rami; (*b*) those with three, or two highly developed rami, or with only one—the corm being reduced to the dimensions of a mere basal segment; (*c*) those reduced to a secondary simplicity (degeneration) by overwhelming development of one segment (e. g. the isolated gnathobase often seen as “mandible” and the genital operculum).

There is no reason to suppose that any of the forms of limb observed in *Arthropoda* may not have been independently developed in two or more separate diverging lines of descent.

Branchiæ.—In connection with the discussion of the limbs of *Arthropods* a few words should be devoted to the gill-processes. It seems probable that there are branchial plumes or filaments in some *Arthropoda* (some *Crustacea*) which can be identified with the distinct branchial organs of *Chætopoda*, which lie dorsad of the parapodia and are not part of the parapodium. On the other hand, we cannot refuse to admit that any of the processes of an *Arthropod* parapodium may become modified as branchial organs, and that, as a rule, branchial outgrowths are easily developed, *de novo*, in all the higher groups of animals. Therefore it seems to be, with our present knowledge, a hopeless task to analyse the branchial organs of *Arthropoda* and to identify them genetically in groups.

A brief notice must suffice of the structure and history of the Eyes, the Tracheæ, and the so-called Malpighian tubes of *Arthropoda*, though special importance attaches to each in regard to the determination of the affinities of the various animals included in this great sub-phyllum.

The Eyes.—The *Arthropod* eye appears to be an organ of special character developed in the common ancestor of the

Euarthropoda, and distinct from the Chætopod eye, which is found only in the Onychophora where the true Arthropod eye is absent. The essential difference between these two kinds of eye appears to be that the Chætopod eye (in its higher developments) is a vesicle enclosing the lens, whereas the Arthropod eye is a pit or series of pits into which the heavy chitinous cuticle dips and enlarges knobwise as a lens. Two distinct forms of the Arthropod eye are observed—the monomeniscous (simple) and the polymeniscous (compound). The nerve-end cells, which lie below the lens, are part of the general epidermis. They show in the monomeniscous eye (see article ARACHNIDA,¹ fig. 26) a tendency to group themselves into “retinulæ,” consisting of five to twelve cells united by vertical deposits of chitin (rhabdoms). In the case of the polymeniscous eye (fig. 23, article ARACHNIDA) a single retinula or group of nerve-end cells is grouped beneath each associated lens. A further complication occurs in each of these two classes of eye. The monomeniscous eye is rarely provided with a single layer of cells beneath its lens; when it is so, it is called monostichous (simple lateral eye of scorpion, fig. 22, article ARACHNIDA). More usually, by an infolding of the layer of cells in development, we get three layers under the lens; the front layer is the corneagen layer, and is separated by a membrane from the other two, which more or less fuse and contain the nerve-end cells (retinal layer). These eyes are called diplostichous, and occur in Arachnida and Hexapoda (fig. 24, in article ARACHNIDA.).

On the other hand, the polymeniscous eye undergoes special elaboration on its lines. The retinulæ become elongated as deep and very narrow pits (fig. 11 and explanation), and develop additional cells near the mouth of the narrow pit. Those nearest to the lens are the corneagen cells of this more elaborated eye, and those between the original retinula cells and the corneagen cells become firm and transparent. They are the crystalline cells or vitrella (see Watase, 7).

¹ This article will be reproduced from the ‘Encyclopædia’ in the next number of this Journal.—E. R. L.

Each such complex of cells underlying the lenticle of a compound eye is called an "ommatidium;" the entire mass of cells underlying a monomeniscous eye is an "ommatæum." The ommatæum, as already stated, tends to segregate into retinulæ which correspond potentially each to an ommatidium of the compound eye. The ommatidium is from the first segregate, and consists of few cells. The compound eye of the king-crab (*Limulus*) is the only recognised instance of ommatidia in their simplest state. Each can be readily compared with the single-layered lateral eye of the scorpion. In Crustacea and Hexapoda of all grades we find compound eyes with the more complicated ommatidia described above. We do not find them in any Arachnida.

It is difficult, in the absence of more detailed knowledge as to the eyes of Chilopoda and Diplopoda, to give full value to these facts in tracing the affinities of the various classes of Arthropods. But they seem to point to a community of origin of Hexapods and Crustacea in regard to the complicated ommatidia of the compound eye, and to a certain isolation of the Arachnida, which are, however, traceable, so far as the eyes are concerned, to a distant common origin with Crustacea and Hexapoda through the very simple compound eyes (monostichous, polymeniscous) of *Limulus*.

The Tracheæ.—In regard to tracheæ the very natural tendency of zoologists has been until lately to consider them as having once developed and once only, and therefore to hold that a group "Tracheata" should be recognised, including all tracheate Arthropods. We are driven by the conclusions arrived at as to the derivation of the Arachnida from branchiate ancestors, independently of the other tracheate Arthropods (see article ARACHNIDA), to formulate the conclusion that tracheæ have been independently developed in the Arachnidan class. We are also, by the isolation of *Peripatus* and the impossibility of tracing to it all other tracheate Arthropoda, or of regarding it as a degenerate offset from some one of the tracheate classes, forced to the conclusion that the tracheæ of the Onychophora have been independently acquired. Having

accepted these two conclusions, we formulate the generalisation that tracheæ can be independently acquired by various branches of Arthropod descent in adaptation to a terrestrial as opposed to an aquatic mode of life. A great point of interest, therefore, exists in the knowledge of the structure and embryology of tracheæ in the different groups. It must be confessed that we have not such full knowledge on this head as could be wished for. Tracheæ are essentially tubes like blood-vessels—apparently formed from the same tissue elements as blood-vessels—which contain air in place of blood, and usually communicate by definite orifices, the tracheal stigmata, with the atmosphere. They are lined internally by a cuticular deposit of chitin. In *Peripatus* and the Diplopods they consist of bunches of fine tubes which do not branch, but diverge from one another; the chitinous lining is smooth. In the Hexapods and Chilopods, and the Arachnids (usually), they form tree-like branching structures, and their finest branches are finer than any blood capillary, actually in some cases penetrating a single cell and supplying it with gaseous oxygen. In these forms the chitinous lining of the tubes is thickened by a close-set spiral ridge similar to the spiral thickening of the cellulose wall of the spiral vessels of plants. It is a noteworthy fact that other tubes in these same terrestrial Arthropoda—namely, the ducts of glands—are similarly strengthened by a chitinous cuticle, and that a spiral or annular thickening of the cuticle is developed in them also. Chitin is not exclusively an ectodermal product, but occurs also in cartilaginous skeletal plates of mesoblastic origin (connective tissue). The immediate cavities or pits into which the tracheal stigmata open appear to be in many cases ectodermic in sinkings, but there seems to be no reason (based on embryological observation) for regarding the tracheæ as an ingrowth of the ectoderm. They appear, in fact, to be an air-holding modification of the vasifactive connective tissue. Tracheæ are abundant just in proportion as blood-vessels become suppressed. They are reciprocally exclusive. It seems not improbable that they are two modifications of the

same tissue elements. In *Peripatus* the stigmatic pits at which the tracheæ communicate with the atmosphere are scattered and not definite in their position. In other cases the stigmata are definitely paired and placed in a few segments or in several. It seems that we have to suppose that the vasifactive tissue of Arthropoda can readily take the form of air-holding instead of blood-holding tubes, and that this somewhat startling change in its character has taken place independently in several instances—viz. in the Onychophora, in more than one group of Arachnida, in Diplopoda, and, again, in the Hexapoda and Chilopoda.

The Malpighian Tubes.—This name is applied to the numerous fine cæcal tubes of noticeable length developed from the proctodæal invert of ectodermal origin in Hexapods. These tubes are shown to excrete nitrogenous waste products similar to uric acid. Tubes of renal excretory function in a like position occur in most terrestrial Arthropoda—viz. in Chilopoda, Diplopoda, and Arachnida. They are also found in some of the semi-terrestrial and purely aquatic Amphipod Crustaceans. But the conclusion that all such tubes are identical in essential character seems to be without foundation. The Malpighian tubes of Hexapods are outgrowths of the proctodæum, but those of scorpion and the Amphipod Crustacea are part of the metenteron or endodermal gut, though originating near its junction with the proctodæum. Hence the presence or absence of such tubes cannot be used as an argument as to affinity without some discrimination. The scorpion's so-called Malpighian tubes are not the same organs as those so named in the other Tracheata. Such renal cæcal tubes seem to be readily evolved from either metenteron or proctodæum when the conditions of the outwash of nitrogenous waste products are changed by the transference from aquatic to terrestrial life. The absence of such renal cæca in *Limulus* and their presence in the terrestrial Arachnida is precisely on a parallel with their absence in aquatic Crustacea and their presence in the feebly branchiate Amphipoda.

We shall now pass the groups of the Arthropoda in review,

attempting to characterise them in such a way as will indicate their probable affinities and genetic history.

SUB-PHYLUM ARTHROPODA.—The characters of the sub-phylum, and those of the associated sub-phyla Chaetopoda and Rotifera, have been given above, as well as the general characters of the phylum Appendiculata which comprises these great sub-phyla.

Grade A.—Hyparthropoda.

Hypothetical forms.

Grade B.—Protarthropoda.

(a) The integument is covered by a delicate soft cuticle (not firm or plated) which allows the body and its appendages great range of extension and contraction.

(b) The paired claws on the ends of the parapodia and the fang-like modifications of these on the first post-oral appendages (mandibles) are the only hard chitinous portions of the integument.

(c) The head is deuterognathous,—that is to say, there is only one prosthomere, and accordingly the first and only pair of hemignaths is developed by adaptation of the appendages of the second somite.

(d) The appendages of the third somite (second post-oral) are clawless oral papillæ.

(e) The rest of the somites carry equi-formal simple appendages, consisting of a corm or axis tipped with two chitinous claws and devoid of rami.

(f) The segmentation of the body is anomeristic, there being no fixed number of somites characterising all the forms included.

(g) The pair of eyes situated on the prosthomere are not of the Euarthropod type, but resemble those of Chaetopods (hence Nereid-ophthalmous).

(h) The muscles of the body-wall and gut do not consist of transversely striped muscular fibre, but of the unstriped tissue observed also in Chaetopoda.

(i) A pair of cœlomoduets is developed in every somite,

including the prosthomere, in which alone it atrophies in later development.

(j) The ventral nerve-cords are widely separated,—in fact, lateral in position.

(k) There are no masses of nerve-cells forming a ganglion (neuromere) in each somite. (In this respect the Protarthropoda are at a lower stage than most of the existing Chætopoda.)

(l) The genital ducts are formed by the enlargement of the coelomoducts of the penultimate somite.

Class (Unica).—ONYCHOPHORA.

With the characters of the grade: add the presence within the body of fine unbranched tracheal tubes, devoid of spiral thickening, opening to the exterior by numerous irregularly scattered tracheal pits.

Genera—*Eoperipatus*, *Peripatopsis*, *Opisthopatus*, etc.

Grade C (of the Arthropoda).—Euarthropoda.

(a) Integument heavily plated with firm chitinous cuticle, allowing no expansion and retraction of regions of the body nor change of dimensions, except, in some cases, a dorso-ventral bellows movement. The separation of the heavier plates of chitin by grooves of delicate cuticle results in the hinging or jointing of the body and its appendages, and the consequent flexing and extending of the jointed pieces.

(b) Claws and fangs are developed on the branches or rami of the parapodia, not on the end of the axis or corm.

(c) The head is either deuterognathous, tritognathous, or tetartognathous.

(d) Rarely only one, and usually at least two, of the somites following the mandibular somite carry appendages modified as jaws (with exceptions of a secondary origin).

(e) The rest of the somites may all carry appendages, or only a limited number may carry appendages. In all cases the appendages primarily develop rami or branches

which form the limbs, the primitive axis or corm being reduced and of insignificant size. In the most primitive stock all the post-oral appendages had gnathobasic outgrowths.

(*f*) The segmentation of the body is anomomeristic in the more archaic members of each class, nomomeristic in the higher members.

(*g*) The two eyes of Chaetopod structure have disappeared, and are replaced by the Euarthropod eyes.

(*h*) The muscles in all parts of the body consist of striped muscular fibre, never of unstriped muscular tissue.

(*i*) The cœlomoduets are suppressed in most somites, and retained only as the single pair of genital ducts (very rarely more numerous), and in some also as the excretory glands (one or two pairs).

(*j*) The ventral nerve-cords approach one another in the mid-ventral line behind the mouth.

(*k*) The nerve cells of the ventral nerve-cords are segregated as paired ganglia in each somite, often united by meristic dislocation into composite ganglia.

(*l*) The genital ducts may be the cœlomoduets of the penultimate or antepenultimate or adjacent somite, or of a somite placed near the middle of the series, or of a somite far forward in the series.

Class 1 (of the Euarthropoda).—DIPLOPODA.

The head has but one prosthomere (monoprosthomerous), and is accordingly deuterognathous. This carries short-jointed antennæ (in one case biramose) and eyes, the structure and development of which require further elucidation. Only one somite following the first post-oral or mandibular segment has its appendages modified as jaws.

The somites of the body, except in Pauropus, either fuse after early development and form double somites with two pairs of appendages (Julus, etc.) or present legless and leg-bearing somites alternating.

Somites, anomomeristic, from 12 to 150 in the post-cephalic series.

The genital ducts open in the fourth, or between the fourth and fifth post-oral somite.

Terrestrial forms with small-jointed legs formed by adaptation of a single ramus of the appendage. Tracheæ are present.

Note.—The Diplopoda include the Juliformia, the Symphyla (*Scolopendrella*), and Pauropoda (*Pauropus*). They were until recently classified with the Chilopoda (centipedes), with which they have no close affinity, but only a superficial resemblance. (Compare the definition of the class Chilopoda.)

The movement of the legs in Diplopoda is like that of those of *Peripatus*, of the Phyllopod Crustacea, and of the parapodia of *Chaetopoda*, symmetrical and identical on the two sides of the body. The legs of Chilopoda move in alternating groups on the two sides of the body; this implies a very much higher development of nerves and muscles in that group.¹

Class 2 (of the Euarthropoda).—ARACHNIDA.

Head tritognathous and diprosthomerous,—that is to say, with two prosthomeres; the first bearing typical eyes, the second a pair of appendages reduced to a single ramus, which is in more primitive forms antenniform, in higher forms chelate or retrovert. The ancestral stock was pantognathobasic, i. e. had a gnathobase or jaw process on every parapodium. As many as six pairs of appendages following the mouth may have an enlarged gnathobase actually functional as a jaw or hemignath, but a ramus is well developed on each of these appendages either as a simple walking leg, a palp, or a chela. In the more primitive forms the appendage of every post-oral somite has a gnathobase and two rami; in higher specialised forms the gnathobases may be atrophied in every appendage, even in the first post-oral.

¹ See the Appendix at the end of the present article, and the accompanying plate.

The more primitive forms are anomomeristic; the higher forms nomomeristic, showing typically three groups or tagmata of six somites each.

The genital apertures are placed on the first somite of the second tagma or mesosoma. Their position is unknown in the more primitive forms. The more primitive forms have branchial respiratory processes developed on a ramus of each of the post-oral appendages. In higher specialised forms these branchial processes become first of all limited to five segments of the mesosoma, then sunk beneath the surface as pulmonary organs, and finally atrophied, their place being taken by a well-developed tracheal system.

A character of great diagnostic value in the more primitive Arachnida is the tendency of the chitinous investment of the tergal surface of the telson to unite during growth with that of the free somites in front of it, so as to form a pygidial shield or posterior carapace, often comprising as many as fifteen somites (*Trilobites*, *Limulus*).

A pair of central monomeniscous diplostichous eyes is often present on the head. Lateral eyes also are often present, which are monostichous with aggregated lenses (*Limulus*) or with isolated lenses (*Scorpio*), or are diplostichous with simple lens (*Pedipalpi*, *Araneæ*, etc.).

Class 3 (of the Euarthropoda).—CRUSTACEA.

Head tetartognathous and triprosthomerous,—that is to say, with three prosthomeres: the first bearing typical eyes, the second a pair of antenniform appendages (often biramose), the third a pair of appendages, usually antenniform, sometimes claw-like. The ancestral stock was (as in the Arachnida) pantognathobasic,—that is to say, had a gnathobase or jaw-process on the base of every post-oral appendage.

Besides the first post-oral or mandibular pair, at least two succeeding pairs of appendages are modified as jaws. These have small and insignificant rami, or none at all,—a feature in which the Arachnida differ from them. The appendages of

four or more additional following somites may be turned upwards towards the mouth and assist in the taking of food.

The more primitive forms (Entomostraca) are anomomeristic, presenting great variety as to number of somites, form of appendages, and tagmatic grouping; the higher forms (Malacostraca) are nomomeristic, showing in front of the telson twenty somites, of which the six hinder carry swimmerets, and the five next in front ambulatory limbs. The genital apertures are neither far forward nor far backward in the series of somites, e. g. on the fourteenth post-oral in *Apus*, on the ninth post-oral in female *Astacus* and in *Cyclops*.

With rare exceptions, branchial plates are developed either by modification of a ramus of the limbs or as processes on a ramus, or upon the sides of the body. No tracheate Crustacea are known, but some terrestrial Isopoda develop pulmonary in-sinkings of the integument. A characteristic comparable in value to that presented by the pygidial shield of *Arachnida* is the frequent development of a pair of long appendages by the penultimate somite, which, with the telson, form a trifold, or when that is small a bifid termination to the body.

The lateral eyes of Crustacea are polymeniscous, with highly specialised retinulae like those of Hexapoda, and unlike the simpler compound lateral eyes of lower *Arachnida*. Monomeniscous eyes are rarely present, and when present single, minute, and central in position.

Note.—The Crustacea exhibit a longer and more complete series of forms than any other class of Arthropoda, and may be regarded as preserving the most completely represented line of descent.

Class 4.—CHILOPODA.

Head triprosthomerous¹ and tetartognathous. The two somites following the mandibular or first post-oral or buccal

¹ Embryological evidence of this is still wanting. In the other classes of Arthropoda we have more or less complete embryological evidence on the subject. It appears from observation of the embryo that whilst the first

somite carry appendages modified as maxillæ. The fourth post-oral somite has its appendages converted into very large and powerful hemignaths, which are provided with poison-glands. The remaining somites carry single-clawed walking legs, a single pair to each somite. The body is anomomeristic, showing in different genera from 17 (inclusive of the anal and genital) to 175 somites behind that which bears the poison-jaws. No tagmata are developed. The genital ducts open on the penultimate somite.

Tracheæ are developed which are dendriform and with spiral thickening of their lining. Their trunks open at paired stigmata placed laterally in each somite of the trunk or in alternate somites. Usually the tracheæ open by paired stigmata placed upon the sides of a greater or less number of the somites, but never quite regularly on alternating somites. At most they are present on all the pedigerous somites excepting the first and the last. In *Scutigera* there are seven unpaired dorsal stigmata, each leading into a sac, whence a number of air-holding tubes project into the pericardial blood-sinus.

Renal cæcal tubes (Malpighian tubes) open into the proctodæum.

Class 5.—HEXAPODA.

Head shown by its early development to be triprosthomeous, and consequently tetartognathous. The first prosthomere has its appendages represented by the compound eyes and a protocerebrum; the second has the antennæ for its appendages and a deutocerebral neuromere; the third has suffered suppression of its appendages (which corresponded to the second pair of antennæ of Crustacea), but has a tritocerebrum and cœlomic chamber. The mandibular somite prosthomere of centipedes has its appendages reduced and represented only by eye-patches (as in *Arachnida*, *Crustacea*, and *Hexapoda*), the second has a rudimentary antenna, which disappears, whilst the third carries the permanent antennæ, which accordingly correspond to the second antennæ of Crustacea, and are absent in *Hexapoda*.

bears a pair of gnathobasic hemignaths without rami or palps, and is followed by two jaw-bearing somites (maxillary and labial). This enumeration would give six somites in all to the head, three prosthomeres and three opisthomeres. Recent investigations (Folsom, 4) show the existence in the embryo of a præmaxillary or supra-lingual somite which is suppressed during development. This gives seven somites to the Hexapod's head, the tergites of which are fused to form a cephalic carapace or box. The number is significant, since it agrees with that found in Edriophthalmous Crustacea, and assigns the labium of the Hexapod to the same somite numerically as that which carries the labium-like maxillipedes of those Crustacea.

The somites following the head are strictly nomomeristic and nomotagmic. The first three form the thorax, the appendages of which are the walking legs, tipped with paired claws or ungues. (Compare the homoplastic claws of *Scorpio* and *Peripatus*.) Eleven somites follow these, forming the abdominal "tagma," giving thus twenty-one somites in all (as in the higher Crustacea). The somites of the abdomen all may carry rudimentary appendages in the embryo, and some of the hinder somites may retain their appendages in a modified form in adult life. Terminal telescoping of the abdominal somites and excalation may occur in the adult, reducing the obvious abdominal somites to as few as eight. The genital apertures are median, and placed far back in the series of somites, viz. the female on the seventh abdominal (seventeenth of the whole series) and the male on the ninth or antepenultimate abdominal (nineteenth of the whole series). The appendages of the eighth and tenth abdominal somites are modified as gonapophyses. The eleventh abdominal segment is the telson, usually small and soft; it carries the anus.

The Hexapoda are not only all confined to a very definite disposition of the somites, appendages, and apertures as thus indicated, but in other characters also they present the specialisation of a narrowly limited, highly developed order

of such a class as the Crustacea rather than a range from lower more generalised to higher more specialised forms such as that group and also the Arachnida present. It seems to be a legitimate conclusion that the most primitive Hexapoda were provided with wings, and that the term Pterygota might be used as a synonym of Hexapoda. Many Hexapoda have lost either one pair or both pairs of wings; cases are common of wingless genera allied to ordinary Pterygote genera. Some Hexapods which are very primitive in other respects happen to be also apterous, but this cannot be held to prove that the possession of wings is not a primitive character of Hexapods (compare the case of the Struthious birds). The wings of Hexapoda are lateral expansions of the terga of the second and third thoracic somites. They appear to be serial equivalents (homogeneous meromes) of the tracheal gills, which develop in a like position on the abdominal segments of some aquatic Hexapods.

The Hexapoda are all provided with a highly developed tracheal system, which presents considerable variation in regard to its stigmata or orifices of communication with the exterior. In some a serial arrangement of stigmata comparable to that observed in Chilopoda is found. In other cases (some larvæ) stigmata are absent; in other cases again a single stigma is developed, as in the smaller Arachnida and Chilopoda, in the median dorsal line or other unexpected position. When the facile tendency of Arthropoda to develop tracheal air-tubes is admitted, it becomes probable that the tracheæ of Hexapods do not all belong to one original system, but may be accounted for by new developments within the group. Whether the primitive tracheal system of Hexapoda was a closed one or open by serial stigmata in every somite remains at present doubtful, but the intimate relation of the system to the wings and tracheal gills cannot be overlooked.

The lateral eyes of Hexapoda, like those of Crustacea, belong to the most specialised type of "compound eye," found only in these two classes. Simple monomeniscous eyes are also present in many Hexapods.

Renal excretory cæca (Malpighian tubes) are developed from the proctodæum (not from mesenteron, as in scorpion and Amphipoda).

Concluding Remarks on the Relationships to one another of the Classes of the Arthropoda.—Our general conclusion from a survey of the Arthropoda amounts to this, that whilst *Peripatus*, the *Diplopoda*, and the *Arachnida* represent terrestrial offshoots from successive lower grades of primitive aquatic Arthropoda which are extinct, the *Crustacea* alone present a fairly full series of representatives leading upwards from unspecialised forms. The latter were not very far removed from the aquatic ancestors (*Trilobites*) of the *Arachnida*, but differed essentially from them by the higher specialisation of the head. We can gather no indication of the forefathers of the *Hexapoda* or of the *Chilopoda* less specialised than they are, whilst possessing the essential characteristics of these classes. Neither embryology nor palæontology assists us in this direction. On the other hand, the facts that the *Hexapoda* and the *Chilopoda* have triplosthomeric heads, that the *Hexapoda* have the same total number of somites as the nomomeristic *Crustacea*, and the same number of opisthomeres in the head as the more terrestrial *Crustacea*, together with the same adaptation of the form of important appendages in corresponding somites, and that the compound eyes of both *Crustacea* and *Hexapoda* are extremely specialised and elaborate in structure and identical in that structure, all lead to the suggestion that the *Hexapoda*, and with them, at no distant point, the *Chilopoda*, have branched off from the *Crustacean* main stem as specialised terrestrial lines of descent. And it seems probable that in the case of the *Hexapoda*, at any rate, the point of departure was subsequent to the attainment of the nomomeristic character presented by the higher grade of *Crustacea*. It is, on the whole, desirable to recognise such affinities in our schemes of classification. We may tabulate the facts as to head-structure in *Chaetopoda* and *Arthropoda* as follows :

Grade *a* (below the Arthropoda).—AGNATHA APROSTHOMERA.

Without parapodial jaws; without the addition of originally post-oral somites to the præoral region, which is a simple prostomial lobe of the first somite; the first somite is perforated by the mouth, and its parapodia are not modified as jaws. = CHÆTOPODA.

Grade 1 (of the Arthropoda).—MONOGNATHA MONOPROSTHOMERA.

With a single pair of parapodial jaws carried by the somite which is perforated by the mouth; this is not the first somite, but the second. The first somite has become a prosthomere, and carries a pair of extensile antennæ. = ONYCHOPHORA (Peripatus, etc.).

Grade 2 (of the Arthropoda).—DIGNATHA MONOPROSTHOMERA.

The third somite, as well as the second, develops a pair of parapodial jaws; the first somite is a prosthomere carrying jointed antennæ. = DIPLOPODA.

Grade 3 (of the Arthropoda).—PANTOGNATHA DIPROSTHOMERA.

A gnathobase is developed (in the primitive stock) on every pair of post-oral appendages; two prosthomeres present, the second somite, as well as the first, having passed in front of the mouth, but only the second has appendages. = ARACHNIDA.

Grade 4 (of the Arthropoda).—PANTOGNATHA TRIPROSTHOMERA.

The original stock, like that of the last grade, has a gnathobase on every post-oral appendage, but three prosthomeres are now present, in consequence of the movement of the oral aperture from the third to the fourth somite. The lateral eyes are polymeniscous, with specialised vitrellæ and retinulæ of a definite type peculiar to this grade. = CRUSTACEA, CHILOPODA, HEXAPODA.

According to older views the increase of the number of somites in front of the mouth would have been regarded as a case of intercalation by new somite-budding of new præoral somites in the series. We are prohibited by a general consideration of metamerism in the Arthropoda (see a previous section of this article) from adopting the hypothesis of intercalation of somites. However strange it may seem, we have to suppose that one by one in the course of long historical evolution somites have passed forwards and the mouth has passed backwards. In fact, we have to suppose that the actual somite which in grades 1 and 2 bore the mandibles lost those mandibles, developed their rami as tactile organs, and came to occupy a position in front of the mouth, whilst its previous jaw-bearing function was taken up by the next somite in order, into which the oral aperture had passed. A similar history must have been slowly brought about when this second mandibulate somite in its turn became agnathous and passed in front of the mouth. The mandibular parapodia may be supposed during the successive stages of this history to have had, from the first, well-developed rami (one or two) of a palp-like form, so that the change required when the mouth passed away from them would merely consist in the suppression of the gnathobase. The solid palpless mandible such as we now see in some Arthropoda is, necessarily, a late specialisation. Moreover it appears probable that the first somite never had its parapodia modified as jaws, but became a prosthomere with tactile appendages before parapodial jaws were developed at all, or rather *pari passu* with their development on the second somite. It is worth while bearing in mind a second possibility as to the history of the prosthomeres, viz. that the buccal gnathobasic parapodia (the mandibles) were in each of the three grades of prosthomerism only developed after the recession of the mouth and the addition of one, of two, or of three post-oral somites to the præoral region had taken place. In fact, we may imagine that the characteristic adaptation of one or more pairs of post-oral parapodia to the purposes of the mouth as jaws did

not occur until after ancestral forms with one, with two, and with three prosthomeres had come into existence. On the whole the facts seem to be against this supposition, though we need not suppose that the gnathobase was very large or the rami undeveloped in the buccal parapodia which were destined to lose their mandibular features and pass in front of the mouth.

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N.B.—References to the early literature concerning the group Arthropoda will be found in Carus, ‘Geschichte der Zoologie.’ The more important literature up to 1892 is given in the admirable treatise on Embryology by Professors Korschelt and Heider.

APPENDIX.

ON THE MOVEMENTS OF THE PARAPODIA OF PERIPATUS, MILLIPEDES, AND CENTIPEDES.

[Matter not contained in the article published in the 'Encyclopædia Britannica.']

I TAKE the opportunity of the issue of my article 'Arthropoda' as a reprint to add to it some drawings showing the movement of the parapodia or legs of Onychophora, Diplopoda, and Chilopoda. I was unable to introduce these into the original article, and I now give them in the form of a plate (Pl. 42). They were made nearly twenty years ago in my laboratory at University College, London, from living specimens by Miss Stone. The live *Peripatus* (*P. capensis*) were given to me by Mr. Adam Sedgwick; the Centipede, *Scolopendra subspinipes* (Leach), was brought to me from Barbadoes by Mr. Tracey; and the Millipede, *Archispirostreptus pyrocephalus* (L. Koch), I obtained from Mr. Pocock.

Of course, the attempt to fix and record, by the simple use of eye and pencil, a phase of successional movement, such as that exhibited by the series of legs of the Arthropoda or of the Chaetopoda, is not altogether satisfactory at the present day. We ought to have records of these phases taken by photography and the instantaneous illumination of the electric spark. But in the meanwhile the drawings, which were carefully and conscientiously made after repeated observation and study, show some interesting facts.

A fact which the drawings are not fitted to show is, that the change of phase—that is to say, the alteration in the

angle formed by the limb and the long axis of the body, appears to proceed from behind forwards in all three cases. Each leg may be considered as resting normally at right angles to the axis of the body. Each is capable of a certain forward swing in the horizontal plane, being provided with a joint and muscles at its base, and of a corresponding backward swing in which the leg passes its first position (that perpendicular to the axis of the body) and makes an excursion or deflection away from the perpendicular in the posterior direction. When the animal is in a state of locomotor activity all the legs steadily swing forwards and backwards through their extreme range of angular displacement, each at the same rate. But they do not all simultaneously assume the same angular position relatively to the axis of the body, nor, on the other hand, do they swing irregularly. They pass consecutively from behind forwards into an identical phase of the swing movement, the leg in front taking up the angular phase just previously exhibited by the leg behind it, which in the meantime has continued its swinging movement, either becoming more deflected or now commencing the return movement. The rate of swing is such that in all cases as yet observed not one great wave occurs but a series of waves are produced, as when wind blows over a cornfield. These waves vary in the number of units (legs) involved in a complete wave according to the kind of Arthropod or Chaetopod under observation. The number of units involved in a "wave" or "swing-group" seems to be fixed in a given species, and not to vary according to circumstances. Whether the rate or relative rate of forward swing is always the same as that of the backward swing (which is that portion of the swing effective in propulsion) has yet to be ascertained, as also the exact excursion made on each side of the perpendicular. Also it would be interesting to ascertain what are the limits of increase and diminution of the rate of swing, and what nervous mechanism, if any, is concerned in its regulation.

These phenomena can only be studied satisfactorily by

photography, and require also the consideration of a large number of forms, such as a representative series of marine Chaetopoda, several genera of Diplopoda, and of Chilopoda, the Phyllopod crustaceans and the higher forms, Hexapod insects and larvæ.

The most important fact which the drawings here published show is that in Peripatus and the Millipede the limbs on opposite sides of the body, which are morphologically related as "pairs," are always in the same phase of fore-and-aft swing; they move together and identically. On the other hand in the Centipede the pairs or opposite limbs on a segment are in phases, which are the extreme opposites in the series of positions through which the limb swings.

Further, it is to be noted in connection with this that the strongly chitinated body of the Millipede takes no part by serpentine movement in the locomotory process; it remains perfectly straight. So, too, the soft body of Peripatus—though it is frequently bent and turned on itself, and may be more or less elongated and contracted at various intervals, yet does not contribute by any serpentine "stroke" to the process of locomotion. On the other hand the Centipede's locomotion is very largely effected by a powerful lateral undulation of the body—groups of three segments being alternately slightly tilted by muscular contraction first on one side and then on the other.

In the case of the Centipede, as already noted, this serpentine rhythmic movement of the body is accompanied by an opposition in the phase of the swing movements of those legs which are paired with one another in a single segment, and a special kind of leg and body movement is the result, with which the special forms of leg-rhythm producing locomotion in other highly-developed Arthropoda (including the tripod action in Hexapoda) might be compared with a view to a mechanical explanation of their genesis.

On the other hand it is worth calling to mind that in some of the large marine Chaetopoda, viz. in Nephthys and Nereis (very few observations on the subject have been recorded)

the process of locomotion (when it takes the form of swimming) is very definitely assisted by a powerful serpentine movement of the whole body left and right, whilst the parapodia exhibit a very rapid (far more rapid than in terrestrial walking Arthropods) swinging action, the phases of which are identical in the paired appendages of either side of a segment, and not antagonistic in spite of the lateral undulation of the body.

One of the important features in the swinging movement of the parapodia of Arthropoda and Chætopoda, which can be observed by simple inspection of the living animal in movement, is the fact that the number of pairs of parapodia involved in a "swing-group" or (as we may put it) the number which one must pass in tracing the phases of movement before one comes to a pair of parapodia in exactly the same phase as that of the pair from which one started, varies in different genera and species. Sometimes the groups may be represented by $a, b, c, d, e, f, g, h, a^1, b^1, c^1, d^1, e^1, f^1, g^1, h^1, a^2, b^2, c^2, d^2, e^2, f^2, g^2, h^2$, where the letters of the alphabet indicate a parapodium in a given phase of swing, and a in the first group is identical in phase with a^1 in the second, with a^2 in the third, and so on. In other cases the groups are represented by two units only— a, b, a^1, b^1, a^2, b^2 , and so on.

In *P. capensis* (Pl. 42, fig. 4) the swing-group number is only two, a, b . The anterior unit a swings forward, whilst the posterior unit b has its claws grasping the surface, and is swinging backwards. As soon as parapodium a approaches parapodium b^1 (and similarly throughout the series) the movement changes, a grasps the surface, and b^1 (and all the others corresponding to it, viz. $b, b^2, b^3, b^4, b^5, b^6$) lets go and commences to swing forward. This is shown in the figures 4, 5, and 6 of Pl. 42.

In the Millipede *Archispirostreptus*, on the other hand, the swing-group number is sixteen, and (as our figures 1 and 2 of Plate 42 show) there are eight of these groups, allowing for peculiarities in the extreme anterior and posterior somites. The regions indicated by the lettering a to f in the

figure are regions where parapodia exhibit the extreme forward swing-phase. They may be called "group-crests." Group-crests are but "phases" in the swinging of the limbs, and they pass along the whole series from behind forward, like the crest of a wave passing along a liquid. Each pair of successive parapodia is in turn the seat of the group-crest, and the waves keep flowing from behind forward with beautiful regularity.

The rate should be measured in different forms, and the conditions affecting the rate of this rhythmic movement should be studied experimentally.

In the Centipede (Pl. 42, fig. 3) the "swing-group" number appears to be six, and the whole phenomenon is profoundly modified by the fact that lateral undulations of the body itself are a definite part of the locomotor activity, whilst the limbs on opposite sides of the same segment are not identical, but antagonistic in phase.

It seems to me probable that the condition presented by the Centipede is a much higher development than that seen in the Millipede, and implies a unilateral differentiation of muscles and nerves which is far from primitive. It may, I think, be reckoned as one of the characters tending to separate the Diplopoda or Prosthogonopora altogether from association with the Chilopods. It would, of course, be very interesting in this connection to have some reliable photographic studies of the phases of parapodial swing in such forms as Scutigera, and, indeed, in all families of Chilopoda.

EXPLANATION OF PLATE 42,

Illustrating Professor Lankester's article on the Arthropoda.

FIG. 1.—Lateral view of a specimen of *Archispirostreptus pyrocephalus* (de Koch) drawn from a living specimen in movement. Magnified twice linear.

FIG. 2.—View of the ventral surface of the same specimen crawling on a glass plate and reflected in a mirror. The letters *a* to *h* indicate the "group-crests" or extreme phases of forward movement, which traverse the series at intervals of sixteen parapodia.

FIG. 3.—Dorsal view of a living specimen of *Scolopendra subspinipes* (Leach) to show the lateral undulation of the body in locomotion, and the grouping of the limbs or parapodia in sixes, which are in antagonistic phases on the two sides of the same segments, but identical with those on the opposite side of the next half-group, *a*, *c*, *e* being in the same phase as *b*, *d*, *f*.

FIGS. 4—9.—Drawings from live specimens of *Peripatus capensis* to show the alternate phases of swing of the parapodia of the same side, and the identity of the phase of the right and left pairs of one and the same segment, also to show the soft-walled nature of the body, its pliability, and considerable powers of extension and contraction.

I should be glad were any of my readers able to inform me as to the name of the author of the following appreciative lines on the subject above discussed.

"A centipede was happy! Till
 One day a toad in fun
 Said, 'Pray which leg
 Moves after which?'
 This raised her doubts to such a pitch,
 She fell exhausted in the ditch,
 Not knowing how to run."

Some Problems of Reproduction.—II.

By

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A.—MULTIPLE FISSION AND EMBRYONIC ENZYMES.

RECENT researches on the utilisation of reserves in plants had shown that in every case examined a ferment or enzyme was present which, under suitable circumstances, could effect in vitro the same process, usually of hydrolysis, which the living organism performs. Thus, if the green cell, under the influence of light, accumulates starch as a reserve during the day, and this starch is removed as a soluble sugar during the night, a diastatic ferment can be isolated from these green cells, and will operate the same conversion. So, too, from germinating seeds we can extract a peptonising ferment which, like trypsin, will hydrolyse proteids into peptones and beyond, yielding leucin, tyrosin, and other amides, such as asparagin. From this consideration on the one hand, and from the observations of Krukenberg, Le Dantec, Miss Greenwood, and A. Dixon and myself on the digestive processes and ferments of Protista of animal habit, it appeared probable that in cases where a cell utilises the reserves stored up in its own interior, enzymes would also prove to be present.

Another consideration had long since been also forced on me by the study of the modes of cellular multiplication. The normal course of the cell is to increase to double its mass, and then to divide at Herbert Spencer's "limit of growth;" yet, how is it that in so many reproductive cells growth

proceeds until they become resting-cells (including the enormous oocyte of the bird), which, when once they cease growing and commence to divide, go on doing so till a brood of small cells is evolved, numerous in proportion to the bulk of the original mother-cell? To find solutions for these problems I made, in the year 1896, a series of preliminary experiments on the developing eggs of the frog and on the extra-vascular blastoderm of the chick; and announced at the Meeting of the British Association of that year that both contained a peptonising ferment, active only in presence of dilute acids. The following year and the year after I tried in vain to confirm these results. I was at a loss to understand these failures till I realised the exceedingly perishable character of such ferments, as pointed out by Reynolds Green. I had, indeed, in the second and third years, kept my tubes in a dark corner, but I had followed the routine of coagulating my material with absolute alcohol, drying, extracting with glycerine, precipitating with alcohol, and working with the precipitate, again dried and re-dissolved. My first year I was able to carry out these processes with but little delay, thanks to the kind help of Mr. E. J. Butler, then my senior scholar (now, 1903, Cryptogamist to the Indian Government); but during the attempts to repeat these observations I was pressed with the routine duties of my chair, and allowed the operations to be protracted over a considerable time; and to this delay I have reason to attribute the successive failures. This year, 1900, I have confirmed my results of 1896.

The frogs' eggs were taken at a time when the segmentation had advanced so far that the white megameres only showed at the blastopores as a small "yolk-plug." They were obtained at first by repeatedly cutting in all directions through the albuminous investment with large sharp scissors, and picking out the eggs singly with a lifter, a laborious and tedious task in which I received much kindly help from some of my students. This year I found a readier method, that of passing the spawn two or three times through an American

mincing machine, which severed the investment, but did not damage the embryos, which slipped through the holes in the plate. Normal salt solution with a drop or two of chloroform or a trace of thymol was then added, and the whole shaken up in a stoppered jar. The envelopes entangled air, and floated for the most part, while the heavier eggs settled. These were drained and crushed, and then put in the incubator in normal salt. The results were negative in neutral or slightly alkaline solutions. In other experiments the solutions were acidulated with 0.3 to 0.7 per cent. HCl.: after incubation from half an hour to twenty hours it was carefully neutralised and boiled to remove any acid albumen. The filtrate, which came through quite clear, was then tested by the biuret test, and in the acid solutions gave a marked reaction, with a trace of cupric sulphate and an excess of caustic-soda solution; that is, a pink colouration identical with that of a few milligrammes of Schuchardt's peptone tested in the same way. The quantities were not adequate to obtain a separation of peptone. In my first attempts I had used the isolated ferment with blood-fibrin washed and boiled, and also with boiled white of egg, and obtained the biuret reaction as above. In this last series I relied on the abundant finely divided proteid reserve granules of the embryo itself as a source of peptone. I added some fibrin, but was unable to ascertain any change in it. A similar isolated batch of frog's eggs kept in a closed locker in the laboratory in thymolised normal salt for three weeks not only gave no peptone reaction, but failed to develop it on incubation.

The technique that I have found most advantageous in obtaining the extra-vascular blastoderm of chicks is to use three- to four-day eggs. These are opened in the usual way, and the embryo removed by cutting with scissors just round the sinus terminalis; I then make a radial cut through the remaining blastoderm and vitelline membrane towards the opposite pole, and take them together in the forceps and shake them apart, first in the dish of salt solution, where I now remove the rest of the vitelline membrane. The blasto-

derm is then transferred to a watch-glass of clean salt solution for a second wash, and then to a test-tube with salt solution to which a trace of thymol or chloroform is added. The supernatant liquid is always cloudy, probably from the separation of yolk granules still adherent to the blastoderm, or from their escape from the inside of the blastoderm-cells after their death. The behaviour of the liquid, with or without obvious fragments of blastoderm, is the same as that with crushed frogs' eggs. When acidulated it has visible little action on added fibrin, but contains enough proteid suspended to show after incubation a good biuret reaction. This is especially well marked when I add more proteid in powder, e.g. a little yolk of hard-boiled egg, treated with alcohol and benzol to remove the oily yellow matters, so as to leave a powder which is nearly white, with no more colour than the dried white would show. After keeping the material in the dark for six weeks, acidulating and adding dried yolk, I only get the faintest of biuret reaction after incubating for twenty hours. This demonstrates the very fugacious nature of the ferment. Guignard noticed that cells of plants which presumably were rich in ferments, as inferred from other reasons, gave a specially deep colouration with Millon's reagent. I find in accordance with this that the extra-vascular blastoderm, carefully washed, is much more deeply stained with Millon than the embryo proper.

There are some peculiarities about the behaviour of the solutions of hen's egg under the biuret test that require a chemist's attention. In some cases I got a dirty feculent precipitate which materially interfered with the ready recognition of the pink colouration. In others, where the solution after the precipitation of the acid albumen still appeared milky, a yellowish scum, like that of white-of-egg dilute solution, save for colour, floated up, and only settled partially and with extreme slowness. In one or two cases in a preliminary set of experiments, of which I omitted to take notes, I got a reddish turbidity on heating, presumably of cuprous oxide; in these cases it occurred that the pink colouration appeared

long before boiling, and then disappeared. The inference is that a saccharoid substance is present in the blastoderm, and an inverting ferment effects its change. It would be most desirable that some more delicate and satisfactory test for the presence of minute quantities of proteoses and albuminoses should be devised or discovered. My chief ground of confidence in my positive results is derived from the failure to obtain them under the circumstances of delay which I have already stated.

The noteworthy fact is that in the frog's eggs the digestion must needs be purely intra-cellular, and is prior to the differentiation of a well-marked gastric layer. I think that the same applies very largely to the blastoderm of the chick; for I have failed to detect proteoses and peptones in the yolk itself on the third and fourth day, while the cells of the blastoderm are themselves gorged with yolk granules, which it seems likely they have absorbed, or rather swallowed amœbafashion.¹

A question that arises here, as in the holozoic Protista, is the origin of the acid required for the peptic digestion and its disposal. Concerning the origin and nature of the acid it is hard to speak; but in the frog, as in the chick, the early formation of the alkaline blood gives a possible clue; or it may be formed by dissociation. As regards the disposal of any excess of acid, I had thought that the alkalinity of the albumen might serve to neutralise the acidity of the digestive juice; but a comparison (using methyl orange as the indicator) of the acidity of the albumen in three eggs that had been incubated for three days with that of three eggs of the same batch kept at the room temperature in this rather cool May revealed no difference.

One thing is clear as the result of this: all probability

¹ The "intra-cellular digestion" of so many of the lower Metazoa must be preceded by a true partial stomachic digestion that causes the food to fall apart into small masses of a size suitable for the endoderm cells to swallow by their pseudopodia.

henceforward is in favour of the view that in the animal, as in the plant, a cell can only utilise its reserves secondarily and mediately—by the internal secretion of an enzyme. We have here to note that the distinction of metabolic processes into the two well-known categories of “anabolic” and “catabolic” is inadequate, for anabolism is not uniform, but twofold.

A cell like the ovarian ovum, receiving dissolved nutriment, builds it up in two modes, in sharp contrast with one another : (1) into protoplasmic matter, inducing protoplasmic growth ; and (2) into food material. The not uncommon assumption that the original formation of reserves is due to the partial breakdown of living protoplasmic substance has, so far as I know, not a spark of evidence to warrant it. We have therefore to distinguish (*a*) “plasmic anabolism,” resulting in growth, and (*b*) “reserve anabolism,” which means the enlargement of a cell through the accumulation of inert products. Such a cell, gorged with inert matter, has not the same need for a corresponding increase of surface as a cell whose protoplasm has enlarged ; and consequently it does not divide. If, however, this cell begins to form an internal enzyme, it can utilise its reserves : its protoplasm grows at the expense of these reserves, and responds to the need of increased surface by dividing. The daughter-cells repeat the same performance till the reserves are utilised. Thus we have the process of brood-formation (“multiple cell-formation,” “sporulation,” “segmentation”), which stands at first sight in such strong contrast to Spencer’s binary cell division at the limit of growth, brought under the same general laws therewith.

The segmenting oosperm is as strongly anabolic as the ovarian egg, but in a different way. To deny its anabolic character because of the necessary antecedent catabolic hydrolysis of its reserves would warrant one in regarding a growing child as mainly catabolic in character because it has to digest its mother’s milk, or the pap supplied by its nurse. The confusion of ideas due to the non-recognition of this distinction of the two forms of anabolism has been responsible

for much brilliant theorising, which of course fails now that we see the double sense of the word.

Before closing I would add a classification of the different modes of brood-division. The first and simplest mode is the "direct" ("enthyschist"): in this case, as seen in the segmentation of the frog's egg, each division of the nucleus is followed by that of the cytoplasm, so that at every stage the brood consists of individual cells. The second is the "delayed" ("bradyschist") type: here the nuclear divisions go on successively without any division of the cytoplasm till the nuclear divisions are completed. Thus the brood-mother-cell passes for a time into the condition of an apocyte, and is finally resolved into single cells by more or less simultaneous segmentation of the cytoplasm. A modification of this process is that of schizogony, which usually occurs when the brood-cells have a particular configuration, like sperms generally and the zoospores of the Coccidians; the cytoplasm around each nucleus grows out almost into the perfect form of the brood-cell to be freed while still continuous with a mass of common cytoplasm, the "cytophore," which may be central, as is most frequent, or eccentric, as in the case of the zoospores of *Noctiluca*, where the cytophore is enormous, and the sperms of many Metazoa. "False brood-formation," takes place where the antecedent is not a single cell, but an apocyte which has discharged living functions, as in the case of the zoosporange of *Saprolegnieæ* or the sporangium of *Mucor*: this becomes resolved into single cells by the cleavage (whether simultaneous or consecutive) of the cytoplasm between the single nuclei. These modes, I think, comprise most of the processes by which single reproductive cells (spores, gametes, etc.) are formed, or colonial aggregations of cells, as in the segmenting oosperm, or the *Volvocineæ*. In eggs provided with abundance of food-yolk, as the hen's egg, there may be a combination of the direct type, giving single cells, and the delayed type, producing the apocytial condition of the yolk below the young blastoderm.

I gave an account of the foregoing facts and theories at the Dover Meeting of the British Association in 1900. The greater part of this essay was typed and the whole of it written out in notes during the autumn of that year. I had kept it by me to form part of a wider discussion ; but I think that it comes fitly into print in company with the following paper on the phenomena of "fertilisation."

B.—AN ESSAY ON FERTILISATION.

At the Southport Meeting of the British Association Professor Hickson, President of Section D, asked me at very short notice to open a discussion on "Fertilisation" in the section, to which I was about to contribute a note on the "Significance of Progamie Fissions." The following pages represent far more closely what I would have wished to say than what I actually said.

The word "fertilisation," like so many others in science, has come down to us from the days of ignorance, undergoing many changes of meaning, and acquiring new meanings by accretion on its way. Undoubtedly it was originally used in the sense in which we speak of a farmer fertilising his land—it conveyed the idea that a female became fertile, or was enabled to bear offspring by a co-operative process on the part of the male, and to this the name was applied. This process is now distinguished, however, as "insemination" or "fecundation;" though in French the term "*fécondation*" has acquired all the meanings of "fertilisation." When, later on, the germ of the young animal was found always to develop from the egg, the idea of the fertilising process was transferred from the mother to the egg; and to-day we use it to denote the process by which the egg, hitherto an inert resting-cell, is induced to become active, and by divisions to give rise to the young life of the germ. At first, we know, this was attributed to a mere emanation, the "*aura seminalis*;" but Spallanzani demonstrated 150 years ago that

the semen must actually come in contact with the egg. By the middle of the last century the change was recognised in all well-studied instances as due to the entrance of a sperm and its complete fusion with the egg.

During the last three decades of the century it was shown that the sperm is itself a cell, and that the fusion is a complete one, cytoplasm to cytoplasm and nucleus to nucleus, so that the germ begins life as a simple 1-nucleate cell, which we term the "oosperm," the equivalent of the "fertilised egg" of common speech. The latter term is falling into disuse from its undue exaggeration of the share of the egg; and is the more to be deprecated as the process is known to be in essence identical with other fusions, known as "isogamous" or "equal conjugations," where the two pairing-cells are similar to the point of identity.

Meanwhile, within the last four or five years, through the revival, principally by Jacques Loeb, of lines of research initiated a decade earlier by the brothers Hertwig, it was found that by treatments of the most varied kinds (mechanical, osmotic, chemical) the eggs of certain Metazoa could be induced to develop without the intervention of the sperm—this result was too rashly called "artificial fertilisation," and was still more rashly invoked as the clue to the meaning of the fusion process which constitutes "fertilisation" in its actual derived sense. Indeed, the lay press was full of marvellous accounts of "chemical fertilisation," for which, perhaps, the enthusiastic professors of the Chicago School are hardly to be held responsible. Yet, as we have seen, this was no misuse of the term in its two older senses—the egg, hitherto infertile, became fertile under the treatment, and started as a germ into a new life. But that sense had become so entirely obsolete that now by common consent we apply to all these cases the uncontroversial term "artificial" or "induced parthenogenesis."

We must remember that in many groups of animals the eggs (or certain types of them) can develop without any co-operation of the sperm; and, indeed, this often occurs in the

Echinodermata, the very group on which the above experiments were chiefly tried. Again, in many lower organisms whose pairing-cells are not differentiated into sperm and oosphere, but are similar, should fusion fail to occur at the right moment, it is not only impossible, but needless; for the single cell will develop individually, its product taking the same course as would have done the product of a fusion (e. g. *Ulothrix*, *Spyrogyra*). Such development, known since the eighteenth century, had received the name of "parthenogenesis." The process is clearly identical in nature with the development of non-pairing resting-cells, such as the resting-spores of Fungi, Algæ, and many Protozoa, to which the term "germination" is applied. This same term is also given to the starting into development of such multicellular bodies as the seeds of flowering plants, and their bulbs and tubers, and similar bodies in higher animals, like the statoblasts of Polyzoa. For germination to take place favourable external conditions are sometimes needed; while in other cases, as with the seeds of the mangroves, there is no pause, and the seed develops as soon as formed. The renewed growth after rest, whether of spores or of seeds, single cells or cell-masses, appears to be due first to the formation of ferments that can dissolve the intra-cellular reserves; and next to the conditions that favour the action of such ferments, and the consequent growth of protoplasm at the expense of the reserves rendered available by digestion. We may henceforward regard all such starting into growth as "germination," reserving the term "parthenogenesis" for the special germination of cells that normally (or rather commonly) are capable of a fusion process with another pairing cell; in other words, "parthenogenesis" is the direct "germination" of a potential gamete.

On the other hand, the development of the resting-cell (of which to us the Metazoan egg is the most familiar type) and the process of cell-fusion are by no means invariably associated together in Nature. True, they are so connected in the cases most familiar to us, but in the bird's egg itself the development of the germ is arrested on laying, and the

“fertilised egg”¹ of the Rotifer, the Green-fly, and the Entomostracan (in marked contrast to the parthenogenetic egg, which develops at once), after a few segmentations, passes into a state of rest, to germinate only after a prolonged rest. The same holds good with the seed of most flowering plants, as I know to my cost, being a raiser of *Abutilons*; the germ forms an embryo of many similar cells, whose development is arrested after a time. Then, only after a lapse of months, it may be, when exposed to suitable conditions—heat, moisture, and aëration,—it starts to grow. The same applies to tubers and statoblasts.

If now instead of counting species of living beings we count types of reproduction, which are so varied in the Protista, the Algæ, and the Fungi, we shall find that in the majority of cases the pairing-cells are naked, but that the fusion-cell immediately invests itself with a complete wall, and either goes to rest itself, or, as in most Sporozoa, divides into a limited number of cells, which themselves pass into the resting state. Indeed, the almost universal formation of a cell-wall around the fusion-cell or oosperm, as soon as the process of fusion takes place in Metazoa and in Metaphytes may be regarded as a survival of this tendency of the cell formed by the fusion of two to pass at once into rest (see below, p. 607). Had our knowledge of reproductive processes been derived from these lower beings, we should never have associated the germination of the resting-cell with the process of cell-fusion.

The word “fertilisation” labours under two disadvantages in its later actual sense, which, historical considerations notwithstanding, must to-day be regarded as its correct sense: (1) in the minds of most naturalists it is still tainted with the idea of what we have differentiated as “germination”—

¹ The term egg denotes four cells morphologically distinct: (1) the ovarian egg; (2) its daughter, the sister-cell to the first polar body; (3) the “matured egg,” sister to the second polar body and daughter of (2); (4) the “fertilised egg,” or oosperm. But, as all four are nearly identical in size and cytoplasm, it is convenient to retain the word “egg” to denote them indifferently.

the scent of the rose still clings to the emptied vessel; (2) it will not conveniently yield an adjective to apply to its modes, etc. This latter objection has been tacitly felt by most writers, who have consequently used the terms "sex," "sexual," etc.—extending this term, which originally implied a binary differentiation, to all cognate phenomena, whether there exist such differentiation or no. Thus my friend Mr. Wager has written a most important and valuable paper on the "Sexuality of the Fungi," though no differentiation of male or female exists in some of the most important and, indeed, primitive types. The word is the more unfortunate, for the user of this terminology is unconsciously swayed by the implicit idea of such binary differentiation into two contrasting categories of beings or cells as exists among ourselves. Yet we have seen that in the most primitive cases the fusing-cells are to all intents and purposes identical—nay, more than two may fuse into a single cell. In isogamy with exogamy, so common in Protista, any one gamete will pair with any other, provided that it belong to a different brood to its own. It has been suggested that here we have a sort of foreshadowing of sexual differentiation, but the suggestion will not hold water for a moment. Let us consider twenty-six broods of pairing-cells matured at the same time, and letter them with the letters of the alphabet, and suppose that their exogamy be a glimmering of sex. Then we may suppose that A is of the male sex, and that with respect to it B, C, D . . . Z, are all more or less females; the same applies to B with respect of C; and in the same way we could show that any one brood is male and female at once—that is, that they are sexually undifferentiated. Therefore, etc., Q, E, D. Again, in the Heliozoan *Actinosphaerium* the pairing-cells are second cousins by the laws of cellular kinship, and have had precisely the same history from the grandparent-cell. The suggestion that there can be any binary differentiation in such cases has arisen simply from the associations inseparable from the word "sex," and the only ground for the assumption of latent differentiations

is the subjective effect of the word on the minds of the writers who have used it in default of a better word. For these reasons I have for some years past never used the word or its derivatives, save where there actually existed the binary differentiation, and then I have prefixed the word "binary" to avoid all ambiguity even to myself. As a substitute I have used the terms "pairing-cells," "pairing-" or "fusion-processes," etc., for all cases where no binary differentiation was necessarily involved or implied. But besides being cumbersome this terminology yields no good derivatives, and hence I venture to propose the term "SYNGAMY" to replace "fertilisation" in its modern restricted sense, which will be followed, I anticipate, in to-day's discussions; and the derivative adjectives "syngamic" and "syngamous" follow naturally. The foregoing discussion is not a mere matter of words, but of the clarification of our thought, which is ever dulled and confused by the use of ambiguous or question-begging words, especially when such are the terms used to designate the main objects of our discussions and of our theories.

It has been suggested that one subject fitly touched upon here would be the function of the centrosome in syngamy. As this organ is as completely absent from Flowering Plants, it can have no import of universal bearing in our general theory; though it has doubtless a partial bearing in Metazoa, where its presence is common. Since, however, even here the centrosome is of varied origin (intra-nuclear or extra-nuclear), and is seen to be formed anew in the parthenogenetic embryos of Echinoderms, its importance must have been much overrated; and we cannot to-day accept the views of those naturalists who have held that the chief function of the sperm is to introduce a centrosome into the egg.

The most common type of syngamy is "cytogamy," the complete fusion of two cells, the "gametes," cytoplasm with cytoplasm, nucleus with nucleus, into a 1-nucleate cell, the "oosperm." In the most primitive cases this union takes place completely and directly; but in some the union is delayed

and incomplete up till the first cell-division, and, indeed, the two constituent halves of the successive nuclei along the new nuclear line may for a long series of divisions show their distinctness more or less defined. This delay is clearly a derived and not a primitive phenomenon, and may be perhaps explained by the acceleration or precocity of the germination of the oosperm in Higher Animals and Plants.

One at least of the two pairing-cells is often the product of a cell-division or a series of one or more preceded by a series of cell-divisions immediately preceding the fusion: these are the "progamic fissions," which we have now to consider. When the syngamy is bisexual, either the male cells or the female cells, or both, may be the produce of such progamic divisions. The special type most familiar to zoologists as universal in Metazoa (with the possible exception of the Alcyonarians) is the so-called "maturation of the egg." The large cell gorged with reserves, produced in the ovary, divides into two, the one with the greater part of the cytoplasm and retaining the "egg" character, the other with a minute cytoplasm, though its nucleus is the counterpart of the other. The former cell then undergoes a similar unequal fission, and the larger cell is now the actual female pairing-cell, or "oosphere," often termed the "mature egg;" and the two small cells are called the "first" and "second polar bodies" respectively (the first polar body may also divide into two). This process may even be delayed until the entrance of the sperm into the egg. At the very commencement of the modern cytological study of fertilisation, in the late '70's, Bütschli, Giard, and Mark independently interpreted these divisions as the reversion to a protistic type of reproduction, to form a brood of four reproductive cells, the one functional, the other three abortive. This view sank into neglect before suggestions made a little later by Balfour and by Minot, who regarded the process as one of elimination into the small cells of something interfering with reproduction by syngamy. An adaptation of their views by Weismann led to the identification with this of over half a score of non-homologous "reduction

processes," and a succession of theories, of which it may suffice to say now that they have had their day. One ground for these theories is the fact that in Metazoa, where progamic divisions were first studied, they are marked by their coincidence with the heterotype mode of nuclear division, and eventuate in the reduction of the number of chromosomes in the pairing-cells to half of that obtaining in the tissue-cells (to be doubled anew by the fusion of two cells to form the oosperm and the new being). When, however, it was seen that reducing divisions occur to produce the tetraspores of the Archegoniate Cryptogams (as also of the Sphacelariæ), which do not pair, but germinate into distinct plants, from the tissues of which the pairing-cells are only produced after long tissue-generations, it became obvious that "progamic fissions" and "reducing divisions" are phenomena distinct, though sometimes coincident, and that a separate explanation was needed for the former.

Oscar Hertwig, in 1890, showed that in *Ascaris* the "maturation divisions" of the egg are absolutely homologous with those that form a brood of four equal sperms in the male. In a paper completed a year later I showed by comparison with numerous data that the view of the three oldest observers was alone tenable. In 1895 Oltmanns described a process in the Wracks (*Fucaceæ*) comparable with the formation of the polar bodies, but of crystalline transparency when the different species were collated.

The oogonial cell always divides into a brood of eight; in some species these are all equal and functional oospheres; in others four (4) are functional and four (4) abortive; in others two (2) are functional and six (6) abortive; in others, again, only one (1) is functional and the other seven (7) are abortive. If additional proof were wanted it was furnished recently by Francotte, who found that certain marine Planarians have exceptionally large "polar bodies," which may be fertilised by sperms like the "matured egg" itself. Thus the morphology of the progamic divisions of the egg of Metazoa is established; and generally such divi-

sions may receive the same morphological explanation, which I will definitely state thus, as I did in 1891: the most primitive pairing-cells are zoospores, produced by brood-formation (multiple cell-division), and their descendants have to be formed in the same way: tissue-cells can never be directly transformed into gametes.

The objection has been justly raised that this gives no adequate reason for the retention of an atavistic process, which could not have survived had there not been some definite physiological good to the race. But a survey of the facts seems to show that cells cannot fuse unless at least one or other of them is fresh from fission, i. e. provided with a young nucleus.

In most isogamous organisms, if the zoogametes fail to pair within a short time of their liberation, from the absence of members of other broods than their own, they become incapable of pairing, and either develop directly, go to rest, or die.

In the isogamous Confervas the zoogametes are usually formed by a cell-division superimposed on those that produce the ordinary non-pairing zoospores: this is indicated by their smaller size and their frequent possession of only half the number of flagella of the others.

The Rhizopod *Trichosphærium* is apocytial: that is, nuclear divisions are not followed by the cleavage of the cytoplasm, so that the organism becomes multinucleate. It exists in two not wholly similar alternating forms, each of which is determined by the resolution of the apocyte into 1-nucleate cells, which escape as zoospores. In the First form, produced from the zygote, these are formed directly by resolution, are incapable of pairing, and grow into the Second form. In the Second form the resolution into zoospores is immediately preceded by the simultaneous mitotic fusion of all its nuclei, and the zoospores are exogamous gametes. In the Heliozoan *Actinophrys* two adults approach: before fusion the nuclei divide, and either mate is divided unequally into a large functional gamete and a small abortive one "polar body." In the fungus *Basidiobolus*,

whose filaments are composed of a single row of cells, multiplying by transverse fission, at a certain moment the cells conjugate two and two: the cells that unite are apparently sister-cells. But this statement needs to be modified: in either cell the nucleus divides by mitosis, and two cousin-nuclei fuse, while the other two are cut off with a trace of cytoplasm as "polar bodies." In most Desmids two adult cells approach to pair, but either divides into two, which fuse respectively with those formed from the other original mate (progamete); so that the actual pairing-cells are not those that approached one another in actual cellular life, but their daughter cells. In the Conjugate *Spyrogyra* the cells fuse by the outgrowth of tubes that meet and anastomose; but the nuclei long remain merely approximated without fusion in the resting-zygospore. It would seem from the results of Chmielewsky that either nucleus at the approach of germination undergoes fission to form a pairing-nucleus and one that aborts, and that it is these daughters of the distinct nuclei of the original pairing-cells that actually fuse at last as gameto-nuclei.

In Diatoms the cells that approach may either divide so as to form two pairs of gametes, as in Desmids, or they may themselves apparently pair; but the process of pairing is only completed after the nuclei have divided once or twice, only one of the daughter-nuclei in either mate being functional, and the rest abortive. Similar divisions produce the pairing-nuclei of the Infusoria, in which the mates (progametes) are also adult.

In other Fungi than *Basidiobolus*, whose isogamous syngamy has been best studied, the Uredineæ and the Ustilagineæ (the Rusts and Smuts) the gameto-nuclei are sister-nuclei of the same undivided cell; but the Basidiomycetes afford so far no support for my present thesis, for the origin of the several (—7) nuclei that fuse to form the nucleus of the basidium is not known to be from recent mitosis.

In cases of unequal fusion the sperms have usually to be produced long in advance and strongly differentiated, so that they are indeed incapable of fission, and consequently

the progamic fissions are usually on the part of the female. Moreover, not to deprive the female of its essential character of size the progamic fissions are usually of the unequal type we have already noted in the Metazoan egg and in some Wracks (as well as in many isogamous forms).

In the Conferva *Edogonium* the oosphere is differentiated by transverse fissions producing a vertical row, of which the upper cell is the oosphere, the rest sterile cells. The same is the case with the Characeæ. Again, in the Archegoniate Cryptogams the sperms have to be formed well in advance to be ready for the conditions for their discharge and travel to the archegone, or flask-shaped body in which lies the central cell. This cell undergoes two divisions, both unequal. The first division early forms a small cell, which lies in the neck (and may again divide), "neck-canal-cell," and a central cell which fills the belly; this last only undergoes its unequal division very late under those very conditions that determine the travel of the sperms. The lower cell is here the oosphere, and the upper is an abortive cell known as the belly-canal-cell from its position at the apex of the belly of the flask.

In Flowering Plants the males and females are really homologous with the corresponding organs of the Cryptogams just mentioned, though certain difficulties of interpretation still exist. The pollen-grain and the embryo-sac are both formed a good while in advance, as each has to be ready on its side for the complicated process of pollination (including the growth of the pollen-tube, and therefore the complex of cells in the embryo-sac) all naked, and including the oosphere, have arisen by early divisions. The pollen contains two nuclei—a "vegetative" and a "generative" nucleus—during the downgrowth of the pollen-tube: the vegetative nucleus is in advance, and is connected with the growth of the tube and travel of the protoplasm; the generative nucleus divides in the tube itself into two, clearly homologous with the sperm-nuclei of the Fern, and are carried down to the embryo-sac without performing any organic function to disturb their condition of youth before fusing with the oosphere. It was the

consideration of the different relations of the progamic divisions in these two cases that led me to lay down as an embracing formula the statement that for fusion one at least of the two nuclei must be fresh from division.¹ This is not yet, I admit, a full physiological explanation, but it is as near to one as we can at present go. It corresponds to what the physicist calls an "interpolation formula." He finds a series of results which, plotted out, give a curve, and that this curve can be expressed by an algebraical formula which embodies all the results obtained, and probably others to be ascertained by fresh experiment, though it would have been impossible to arrive at such by *à priori* reasoning. And with such formulæ we have often to be content as representing a distinct advance for the time in that systematisation of knowledge which we call science.

An opinion broached in my 1891 paper which met with the greatest opposition, not to say discredit, was that nuclei contained in the same cytoplasmic investment, as, for instance, those of the *Saprolegniæ*, might fuse, and so effect a truly syngamous process (endokaryogamy). Nowadays the cases of the *Basidiomycetes*, most *Ascomycetes*, the *Ustilagineæ*, and the *Uredineæ* are very widely regarded as syngamous. And the conjecture of Boveri that certain cases of apparent parthenogenesis when only one polar body was formed might be truly syngamous, the nucleus of the imperfectly detached second polar body moving back and fusing with that of the oosphere, and so taking the place and the rôle of a sperm, has been brilliantly confirmed by Brauer who has followed up the details in the brine-shrimp *Artemia*. As we have seen, the second polar body is undoubtedly morphologically an oosphere, and can in some cases be "fertilised" (*sit venia verbo*) by a sperm. This favours Maupas's view that in the actual process of syngamy there is neither "male" nor "female," but that sex is a mere adaptation of the cytoplasm

¹ In many *Coccidiaceæ* a partial disruption of the nucleus of the "egg," and the expulsion of its fragments, replaces the unequal fission with the formation of functional oosphere and rudimentary polar body.

to ensure on the one hand a sufficiently large amount of cytoplasm and reserves to the young, and on the other enough mobility on the part of one gamete to ensure its finding the other and to favour crossing.

A very remarkable type of syngamy was first discovered by Boveri, as long ago as 1889. He found that the egg of Echinids, when shaken up, divides into fragments, only one of which can be nucleated; that sperms enter whether these contain the nucleus or no; and that development follows in either case. These experiments have been recently taken up and extended, notably by Delage, who has given the name of "merogony" to the process. Giard, however, has regarded it as really a parthenogenesis of the male which, when reduced to a differentiated sperm, has not sufficient cytoplasm for independent life. However, this assumes that the cytoplasm plays no part of its own in cell-life, but lies absolutely under the despotism of the nucleus—a view for which evidence is absent. True this differentiated sperm has but a minute investment of cytoplasm, but, such as it is, it in Metazoa contains the centrosome, and may in other respects as in this have the power of growing within the egg at the expense of the female cytoplasm and reserves during the very process of fusion therewith. Male parthenogenesis, strictly speaking, can only exist where the sperm is slightly smaller than the oosphere, the binary sexual differentiation is not too complete; and the term should be reserved for such cases of what may be called "anisogamy," which are notably to be found in certain Algæ.

Lankester regards the independent germination of small zoospores as a case of male parthenogenesis, in cases where they never show any signs of pairing, and occur in a distinct stage of the life-cycle, as in *Hæmatozoic Coccidia*; but this seems to be an inversion of the facts. For pairing-cells assuredly, originated from indifferent zoospores, which germinate independently; and where there is no symptoms of such zoospores being sperms gone wrong, we are not justified in supposing it.

Merogonic fertilisation has been obtained also by cutting the egg in pieces and by piercing the vitelline membrane so that a portion of the egg cytoplasm protrudes and is separated off as an "extra-ovate." The remarkable condition of the egg in *Aleyonium*, where Hickson tells us that the nucleus disappears completely as the egg matures, suggests that in this group the germ-nucleus is entirely of spermatogenic origin as in artificial merogony. Clearly we cannot speak of "merogony" where the entire egg is present to receive the sperm if we pay any attention to the etymology of this word, and it is hardly old enough for us to forget it. But the essence of merogony is that the cytoplasm of the germ is in this case almost wholly of maternal origin (with the above reservation) and the nucleus is wholly male. Therefore an *Aleyonian* germ before segmentation, from which the unimportant ablation of a portion of the cytoplasm had been made, would be exactly equivalent to the merogonic germ of an Echinoderm. We will refrain from the creation of a new term to cover this process.

We have been accustomed to regard the presence of double the number of chromosomes in the germ and its offspring down to the new reducing divisions as resulting from the fusion of the two pairing-nuclei. Nay, in some cases at least, the fusion of the nuclei may be hardly complete, and this partial independence may long persist in the developing-cells of the embryo. On the other hand, Delage has recently shown that in all embryos of Echinoderms, whether from oosperms, from parthenogenetic eggs with one polar body, or from mature oospheres that have formed two polar bodies, as well as from merogonic syngamy, the number of chromosomes is the full (double) number characteristic of the adult and of the unreduced reproductive cells. Yet in the case of the mature parthenogenetic oosphere, and in the merogonic germ, the start is made with the half number of chromosomes; and the nucleus must therefore have the power of doubling them so as to suit the needs of the germ, which is habitually formed by cytogamy, and so normally possesses the doubled number.

With regard to the function of syngamy, taking the widest sense of the word, the only general formula that will cover the facts is that it effects a cellular reorganisation that can be effected in no other way. In many cases it takes place between cells or nuclei related by the closest bonds of cellular kinship, which is so much closer than Metazoan kinship. Where, however, the gametes are of different parentage, it undoubtedly, on the one hand, tends to breed out individual deviations from the norm, as Strasburger holds; and, on the other, it produces new combinations of individual variations which offer wider fields for natural selection, as Weismann postulates. Finally, I would urge that no real advance can be made in any branch of science as long as we use words without a precise meaning attached to them; and that we only hinder advance so long as we base theories of the most wide-reaching significance on facts obtained in a very limited field (such as, for instance, the study of reproductive processes in the Metazoa), so long as we use such theories as Procrustean beds on to which we seek to make all other facts fit, whether by lopping them where they prove too much, or by stretching them where they prove too little. For these reasons, as a student of plant and protistic life, as well as of that of animals, I am grateful for the opportunity that my friend, the President, has given me of addressing Section D on the subject of fertilisation.

Summary.

1. The term fertilisation as actually used is too ambiguous for scientific precision.
2. In its first and older sense it denotes the starting into active cell-life and multiplication of a resting-cell, and should properly be regarded as one case of germination. The parthenogenetic development of eggs under chemical and mechanical treatment falls under this category.
3. In its second sense, regarded now-a-days as the "strict"

sense, it denotes a process of cellular (or nuclear) fusion, and is better designated as "syngamy."

3. The terms "sexuality, sexual," etc., have been used also ambiguously, and would be advantageously (*a*) replaced by "syngamy" and its derivatives where no binary differentiation is necessarily implied, or (*b*) only used with the prefix "binary" where such differentiation is intended.

4. Syngamy is not necessarily associated with germination; on the contrary, in the most primitive types the cell freshly produced by syngamy (the zygote) passes into a condition of rest, or gives rise only to a limited brood of resting-cells, which will only germinate after the lapse of time and under favourable conditions. The formation of a membrane round the oosphere at the onset of syngamy in Metazoa and Metaphytes is probably the last trace of this, the original consequence of syngamy.

5. Syngamy includes internal karyogamy and merogony as well as the pairing of separate individual cells. It seems possible that in the Alcyonarians the oosphere is non-nucleate, and that the nucleus of the oosperm is exclusively male, as in that produced by merogony.

6. Progamic cell-divisions come under three formulæ:

(*a*) Gametes are morphologically equal to zoospores, and are therefore produced by multiple cell-divisions.

(*b*) No tissue-cell ever becomes directly transformed into a gamete.

(*c*) Karyogamy (with the possible exception of the Basidiomycetes) is never possible where both the pairing-cells (or nuclei) have had a share in active cell-life or growth.

7. Progamic divisions and reducing divisions, though sometimes coincident (as in Metazoa), are not necessarily associated, but may be widely divided in the life-cycle where there is "antithetic alternation of generations."

8. The germ formed by parthenogeny or merogony can double the number of its chromosomes,

C.—THE RÔLE OF THE SPERM.

This has been a matter of much debate. One school sees in it merely the bearing-in of the ferment that starts* the oosperm into development, or of a new centrosome to the oosphere which has lost its own during the formation of the polar bodies. Another school refuses to consider anything but the male nucleus, which indeed constitutes the bulk of the sperm at its entrance. Others, again, insist that however small be the cytoplasm of the sperm in quantity, it is by no means negligible in quality. A consideration of the facts as presented in Nature, and described and figured concordantly by numerous trustworthy observers, will convince us that the third view is a decided under-statement of the case.

The minute size of the sperm with its bare envelope of cytoplasm are correlated with the presence of large stores of unorganised reserves in the egg. When it enters, its nucleus is so concentrated and condensed that it cannot fuse with the female nucleus until it has attained a more normal condition, and for this it must be nourished.

The first function, therefore, of the sperm on entering the egg is to procure this nourishment for itself, which it does by digesting some of the reserve of the egg; whereupon the cytoplasm of the sperm with its centrosome grows even more rapidly than its nucleus, till the organised living matter of the oosperm is seen to be largely constituted by this growth of the male element. This is clearly shown in the exquisite figures of Wilson (1) (Echinoderms) and Vejdovsky (2) (Oligochaetes).

Now we must insist that the yolk-granules are not living matter at all, but mere inclusions within the living cell, absolutely comparable to starch granules. The nature of protoplasm is not determined by its food, but by its origin, so that the fact that the male cytoplasm grows in this way within the egg does not lessen its essential maleness.

Complete conjugation only takes place, we may say, with

the formation of the segmentation spindle when the male cytoplasm is probably equal in bulk to the female.

We have noted above that the oosperm in primitive types of syngamy has usually the character of a resting-cell, whereas the fertilised egg of binary sex immediately undergoes brood-division (segmentation). The key to this difference probably lies in the fact just recapitulated. Since the sperm must grow for the conjugation to take place and secrete an enzyme to digest the food granules, the female cytoplasm itself must also grow in presence of this digested food, as is clearly shown in the figures we have referred to. We have seen that such growth at the expense of intra-cellular reserves is the starting-point for brood-division in general. Thus the impulse for division given by the sperm is no essential phenomenon of syngamous union; it is conditioned by the differentiation of binary sex, and is the indirect consequence of that reduction of the sperm which makes its growth within the egg the necessary prelude of complete fusion therewith.

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INDEX TO VOL. 47,

NEW SERIES.

- Actinotrocha larva, body-cavities and nephridia of, by E. S. Goodrich, 103
- Arthropoda, the structure and classification of, by Lankester, 523
- Ascidian, a new Molgulid, by Bourne, 233
- Bernard, studies in the retina, Part VI, 303
- Bourne, Gilbert C., on a new Ascidian of the family Molgulidæ, 233
- Convoluta roscoffensis*, the bionomics of, by Gamble and Keeble, 363
- Cymonomus, modification of eye peduncles in, by Lankester, 439
- Distomum cirrigerum* by Warren, 273
- Enteropneusta from Madras, by K. R. Menon, 123
- Evans on *Peripatus guianensis*, 145
- Eye peduncles of crabs of the genus *Cymonomus*, by Lankester, 439
- Fin-rays of fishes by Goodrich, 465
- Fishes, dermal fin-rays of, by Goodrich, 465
- Fishes, ovarian ova of, by Wallace, 161
- Fowler on *Planktonetta atlantica*, 133
- Gamble and Keeble on the bionomics of *Convoluta roscoffensis*, 363
- Goodrich on the body-cavities and nephridia of *Actinotrocha* larva, 103
- Do., on the dermal fin-rays of fishes, living and extinct, 465
- Hanna on trypanosoma in birds from India, 433
- Hansen on the genera and species of *Symphyla*, 1
- Hartog on some problems of reproduction, 583
- Keeble and Gamble on the bionomics of *Convoluta roscoffensis*, 363
- Koenenia, a new species of, from Texas, by Augusta Rücker, 215

- Lankester, E. Ray, on the modification of the eye peduncles in crabs of the genus *Cymonomus*, 439
- Do., on the structure and classification of the Arthropoda, 523
- Menon on Enteropneusta from Madras, 123
- Nephridia of *Actinotrocha* larva, by E. S. Goodrich, 103
- Oligotrema psammites*, a new Ascidian, by Gilbert C. Bourne, 233
- Ovarian ova of Teleostean and Elasmobranch Fishes, by Wallace, 161
- Peripatus guianensis*, by Richard Evans, 145
- Planktonetta atlantica*, by Fowler, 133
- Reproduction, problems of, by Hartog, 583
- Retina, studies in, by Bernard, Part VI, 303
- Rücker on a new *Koenenia* from Texas, 215
- Symphyla, the genera and species of, by H. J. Hansen, of Copenhagen, 1
- Trypanosoma* in birds, by Hanna, 433
- Warren on the anatomy and development of *Distomum cirrigerum*, 273
- Wallace on the ovarian ova of Teleostean and Elasmobranch Fishes, 161

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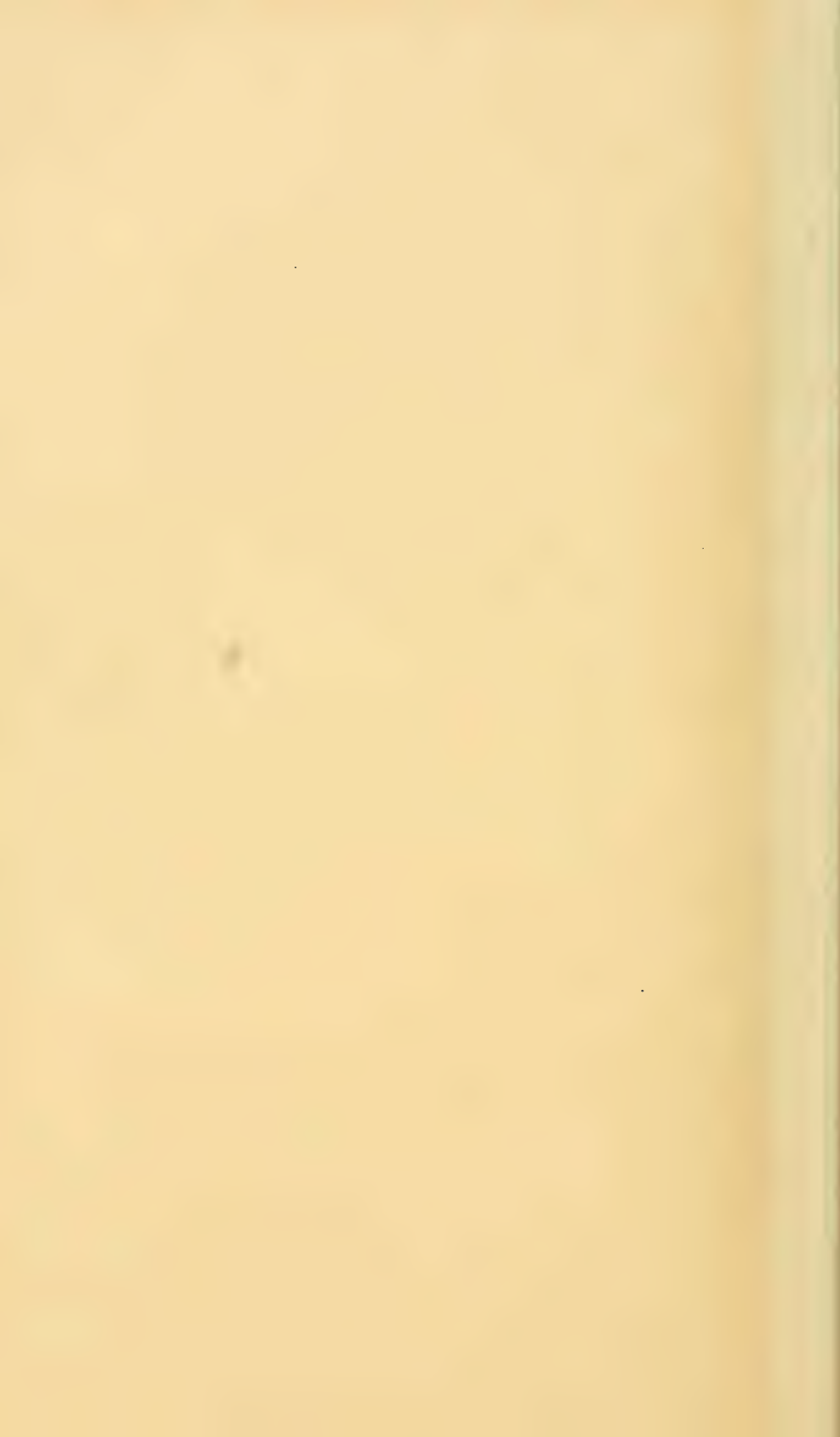
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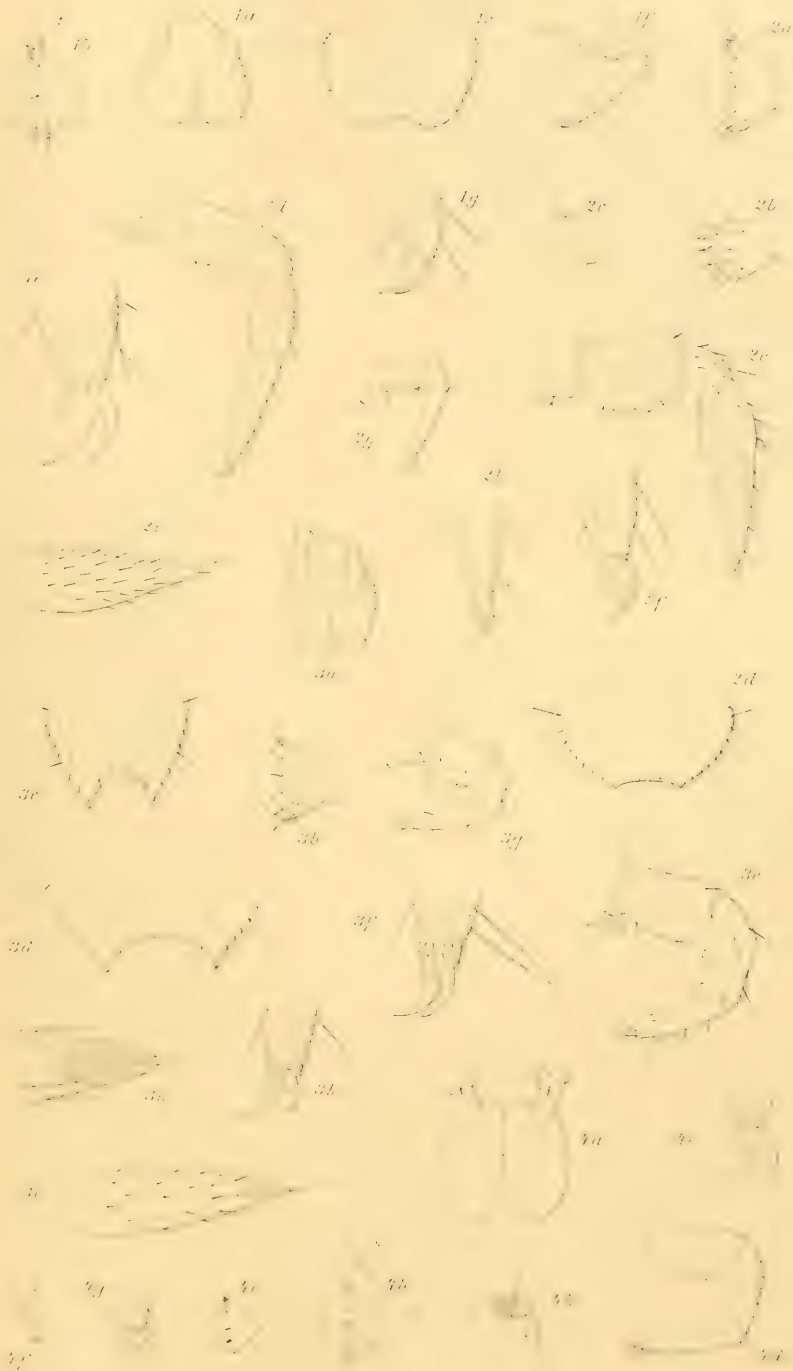


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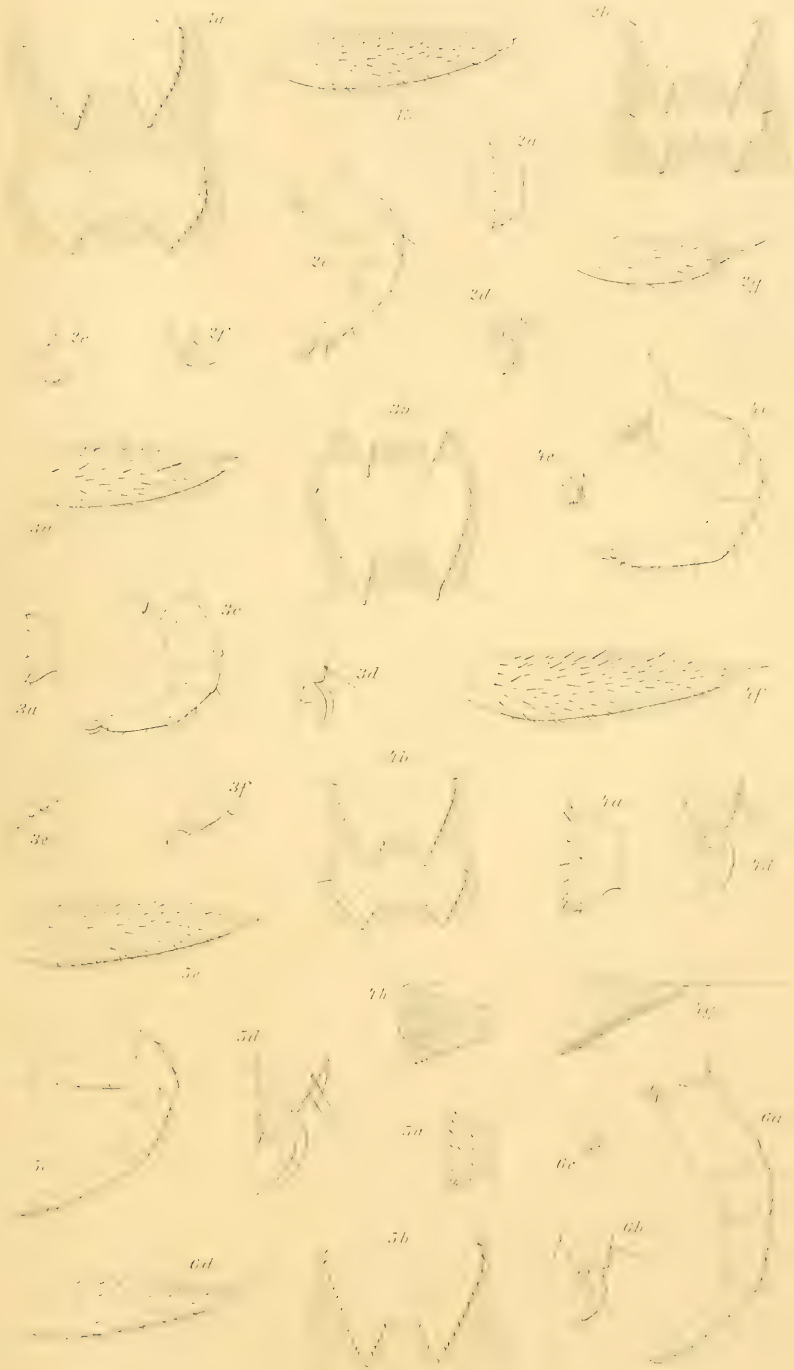
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Fig. 1



Fig. 4



Fig. 3

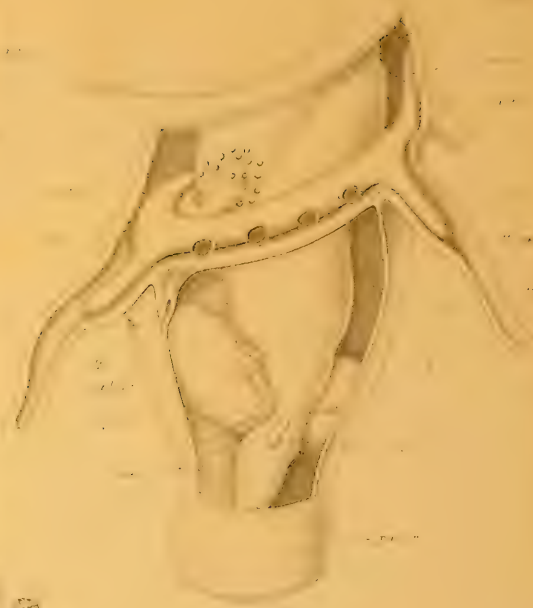


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Fig. 5

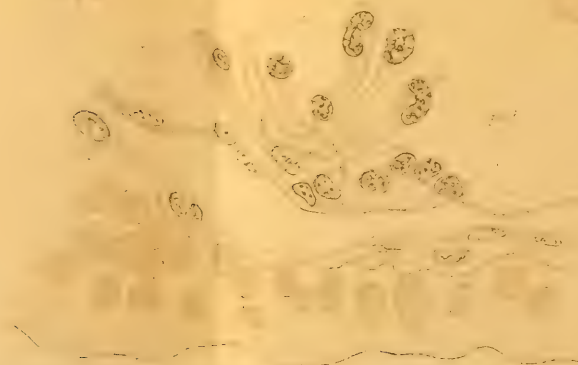


Fig. 6



Fig. 7



Fig. 8



Fig. 9.



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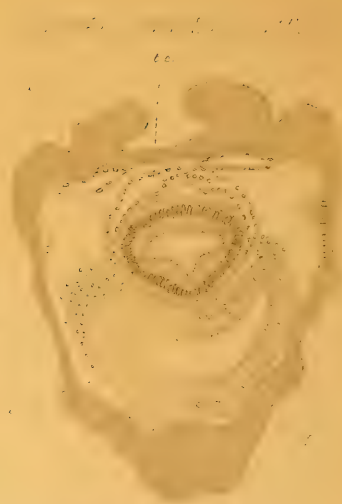


Fig. 12.



Fig. 10.



Fig. 13.



Fig. 14.



Fig. 15.

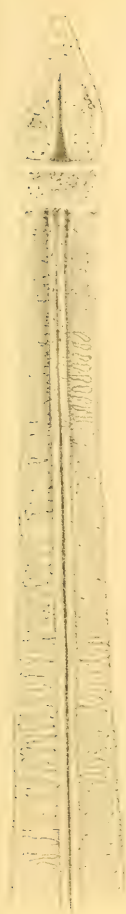


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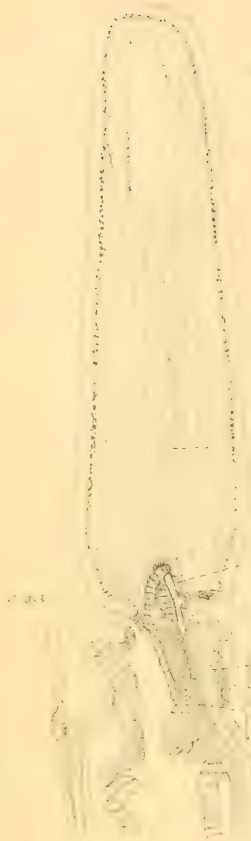


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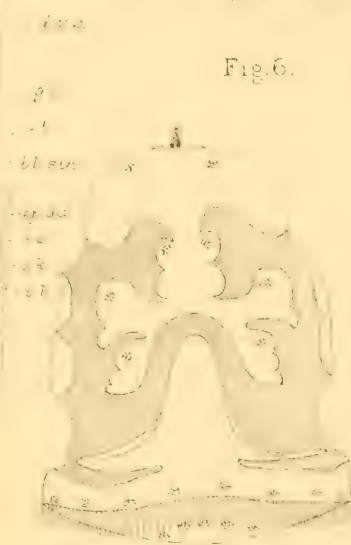


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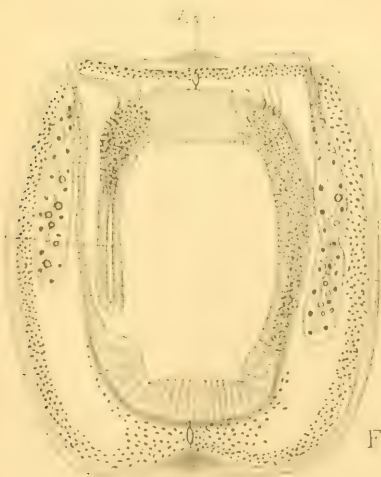


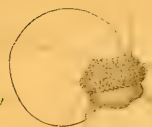
Fig. 4.



Fig. 2.

Oral.

Fig 1



Anterior

Aboral
Anterior

Left

Right

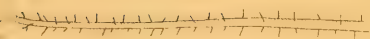


Fig 2

Posterior



Fig 3



G.H. Fowler del

Fig 7



l.

Posterior.
Fig 6.

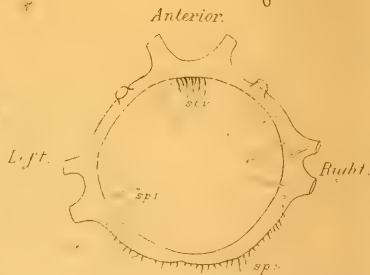


Fig 8.



Aboral.

Anterior

Oral.



Fig 10.

Posterior.



Fig 9.

Aboral

Anterior

Oral

Left

Right

Aboral

Fig 5.



Fig 11.

Hutchings London.

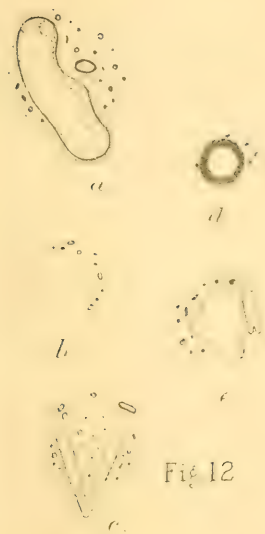


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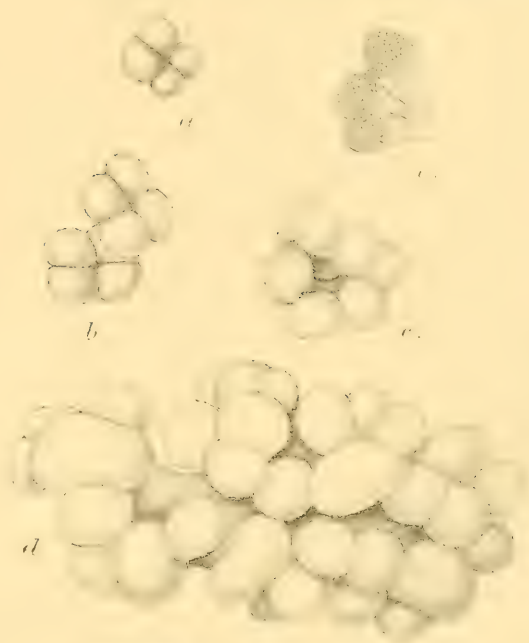


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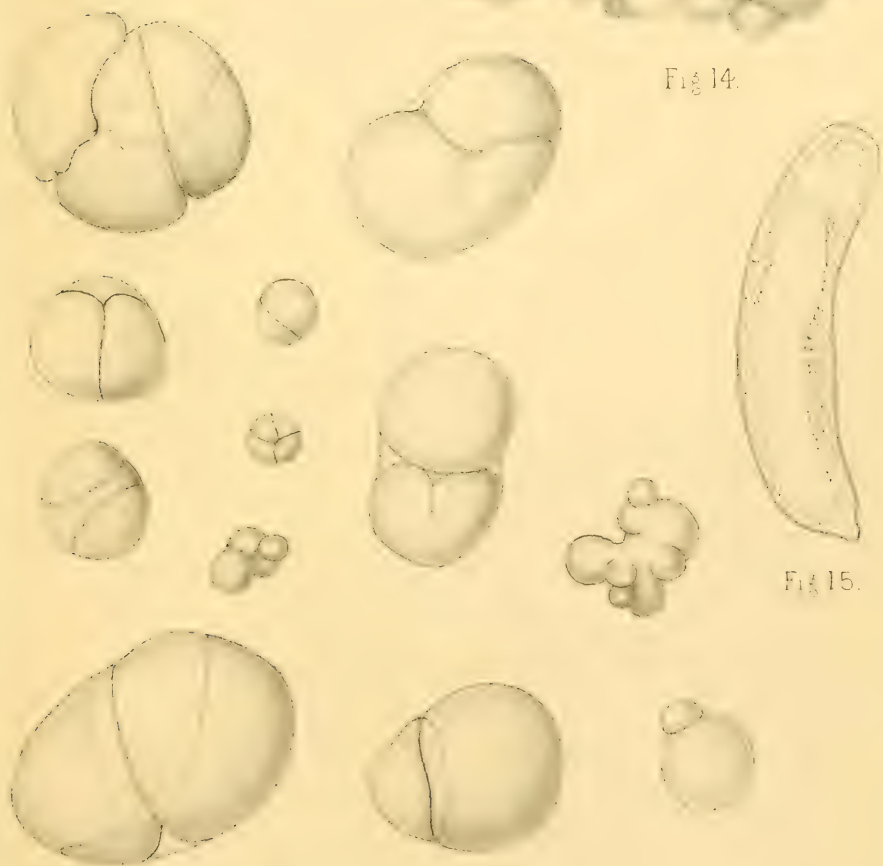
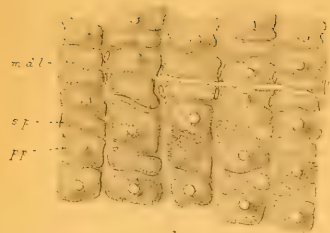
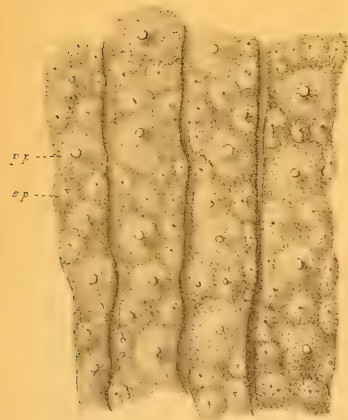


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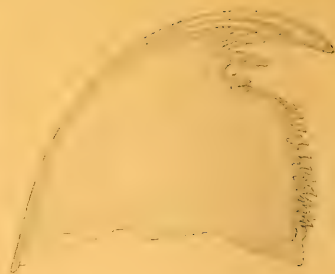
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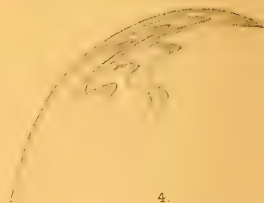
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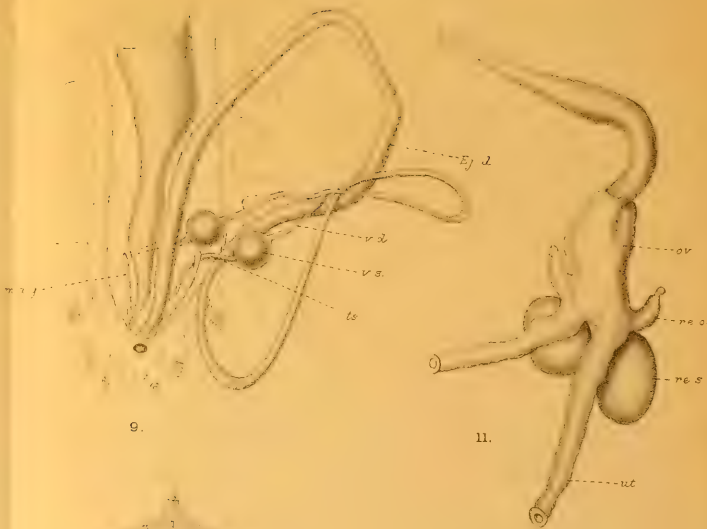
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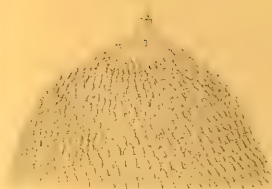


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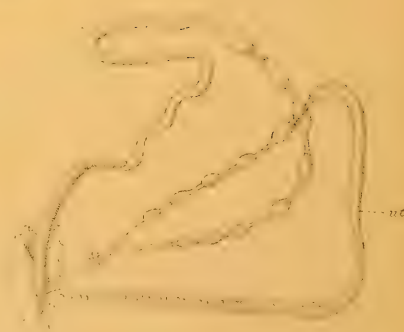
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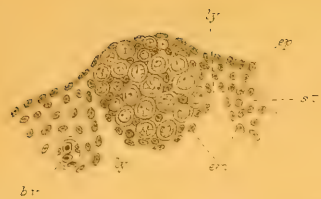


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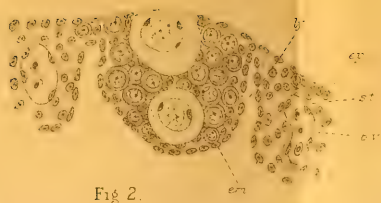


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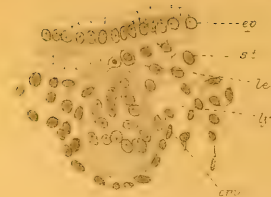


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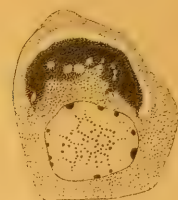


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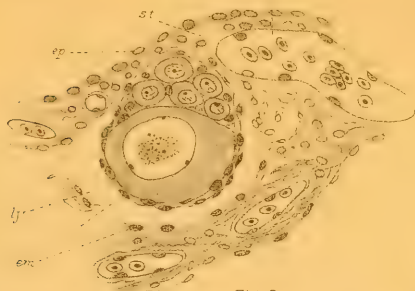


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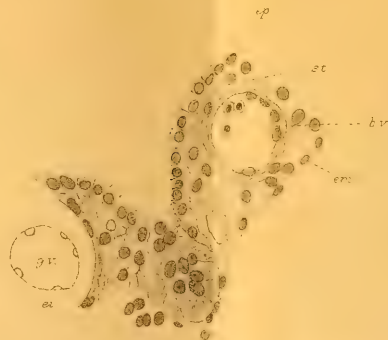


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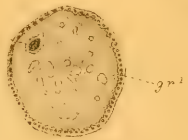


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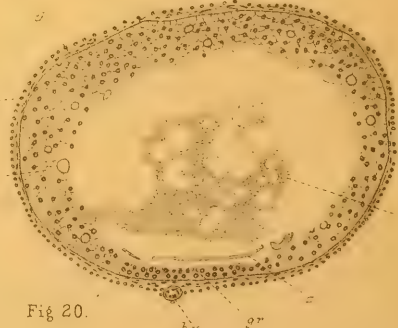


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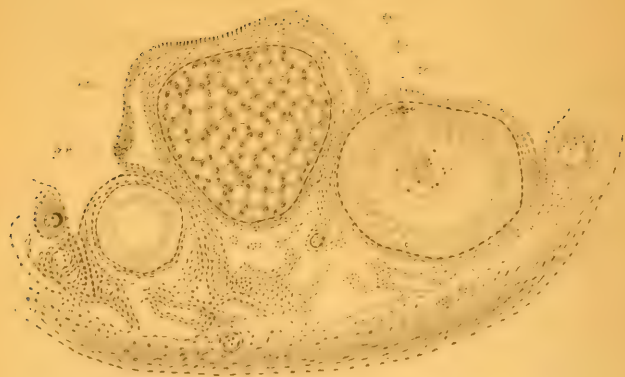


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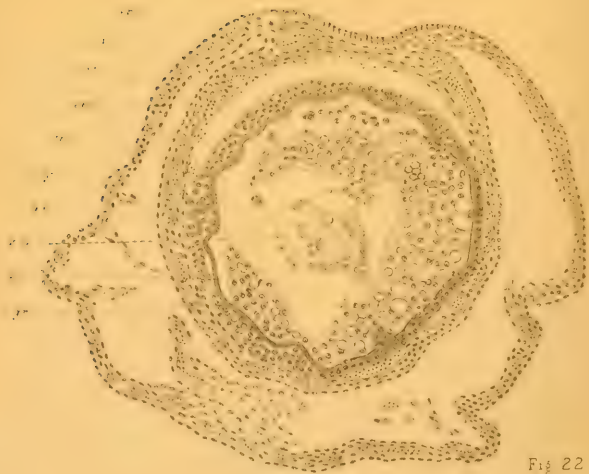


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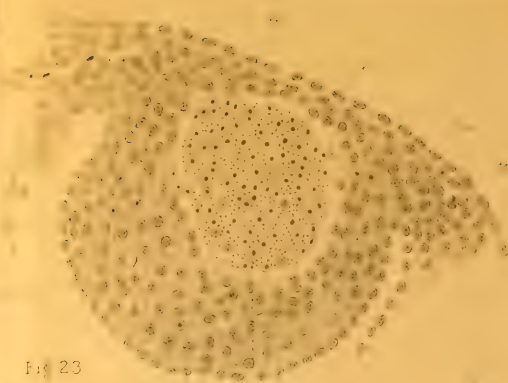


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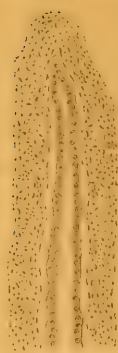


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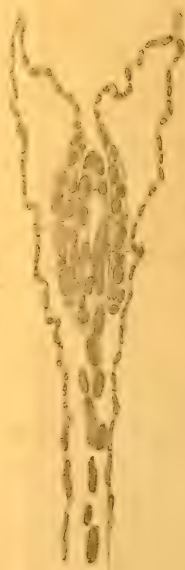


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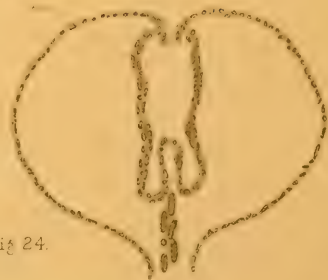


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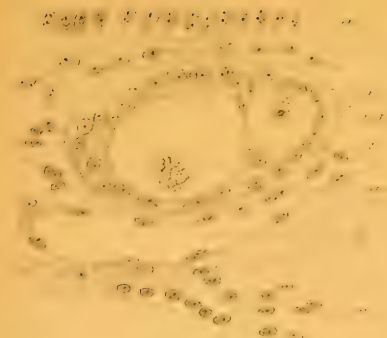


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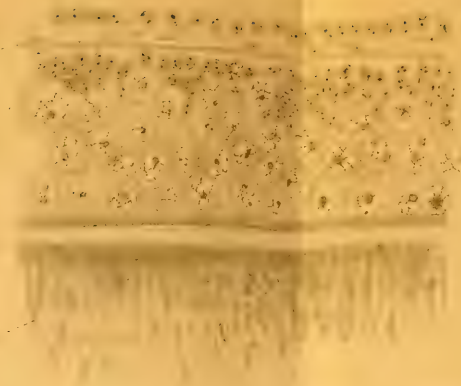


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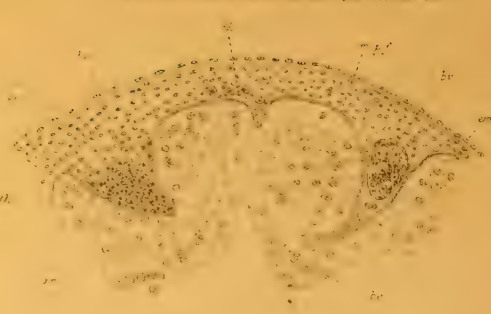


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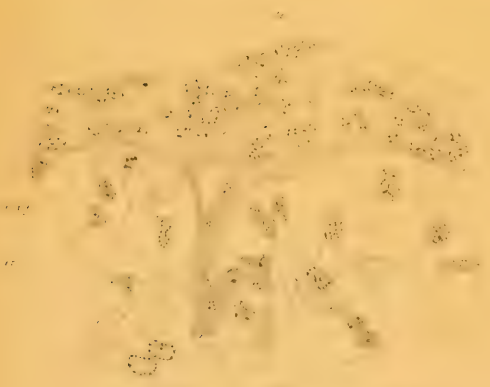


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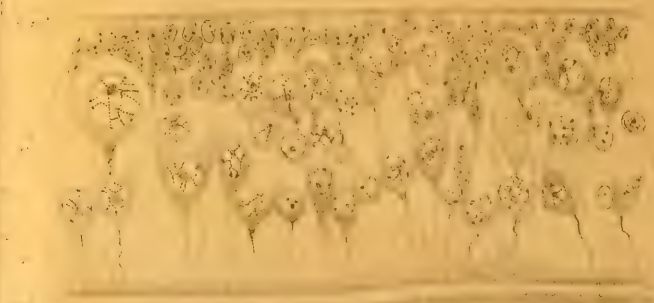


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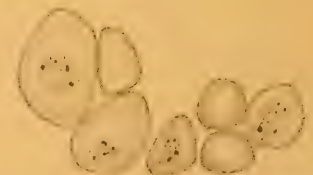


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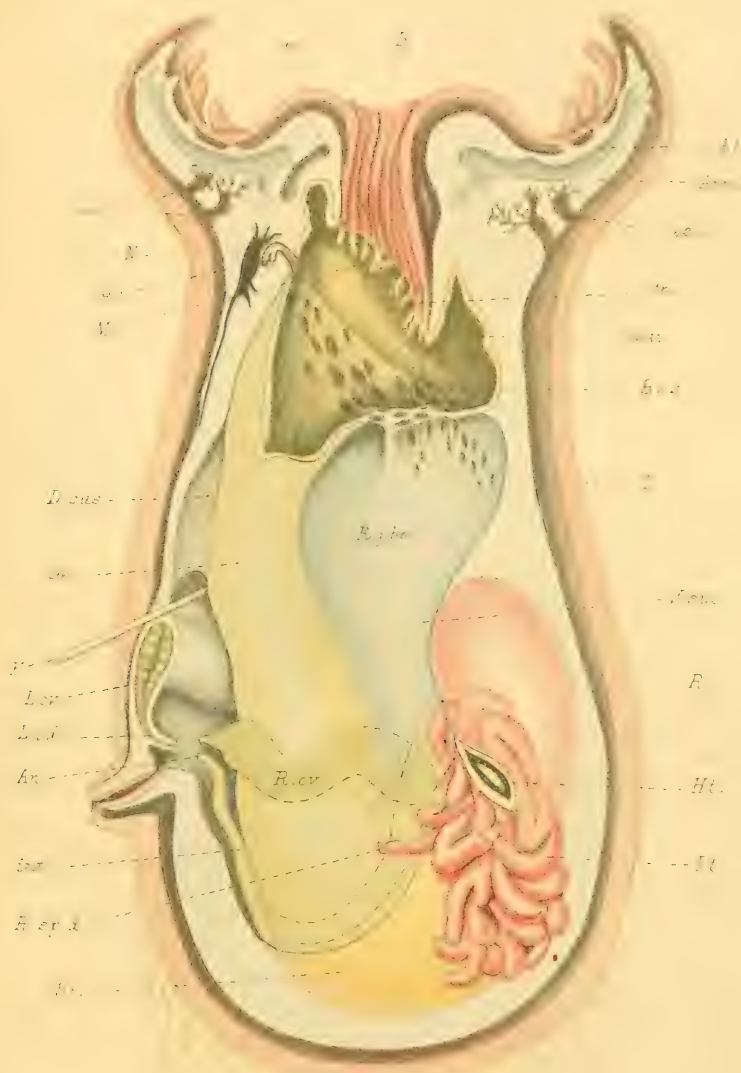


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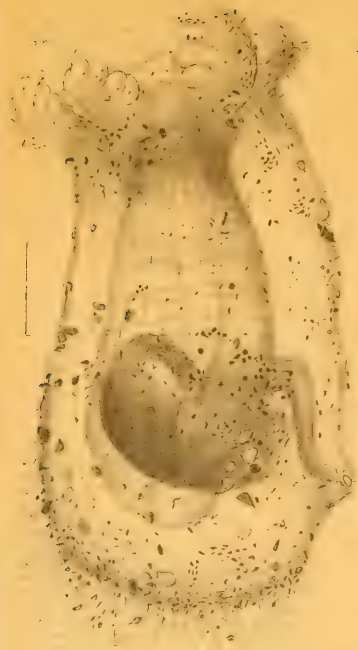


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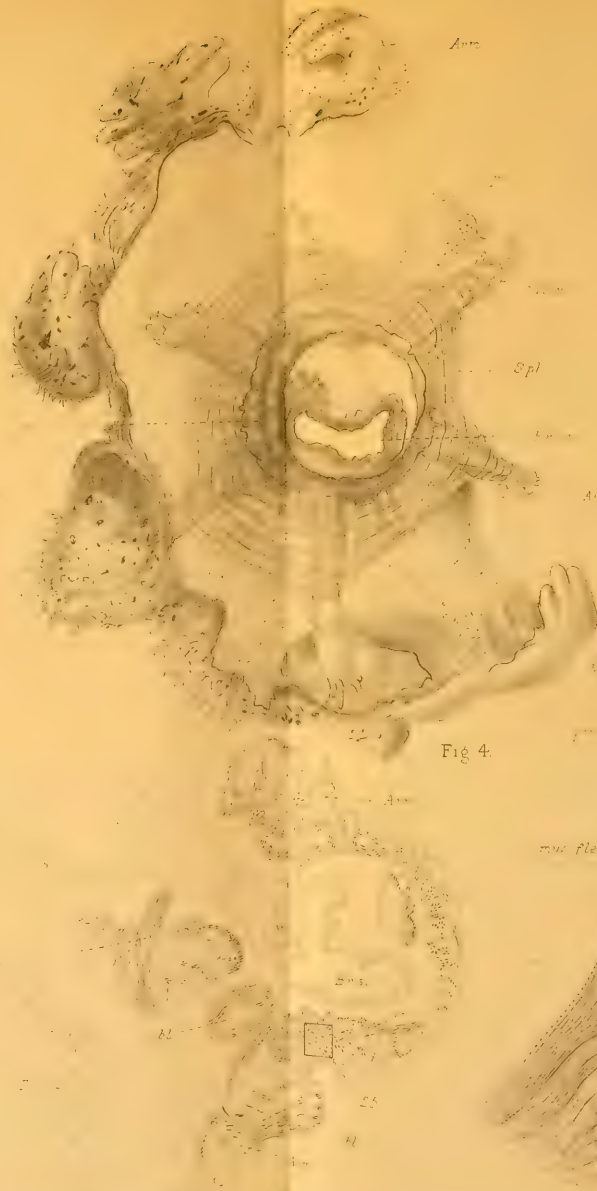


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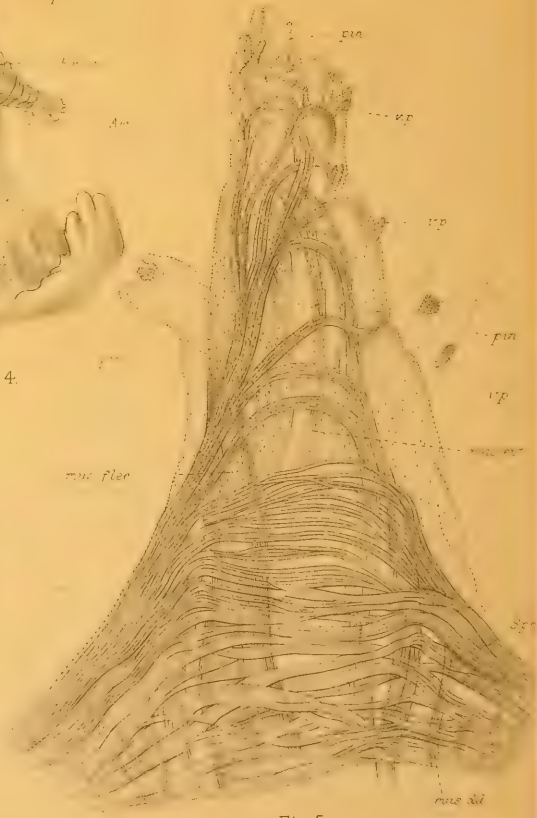


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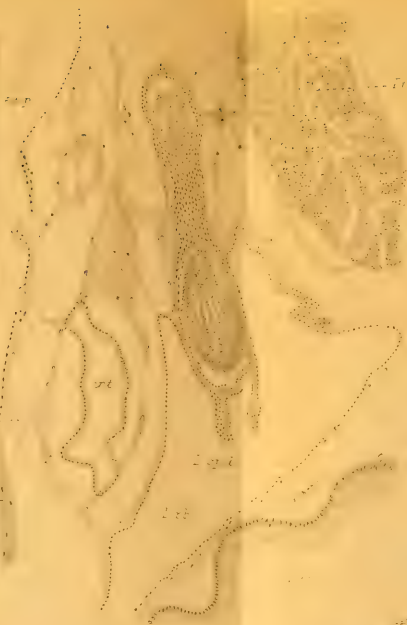


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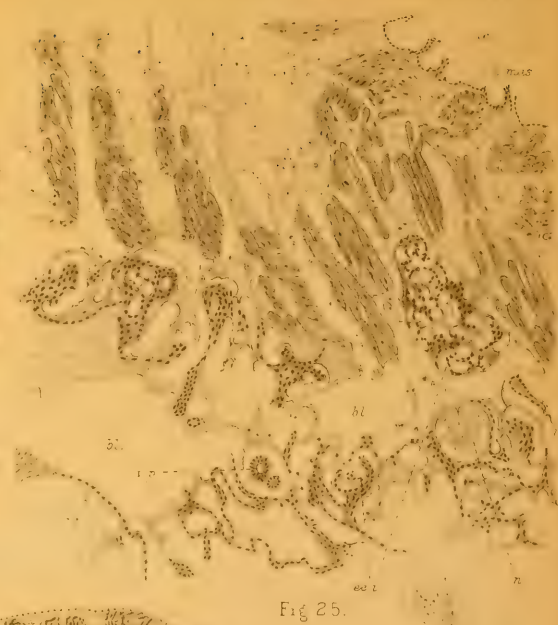


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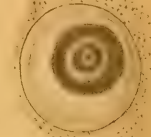


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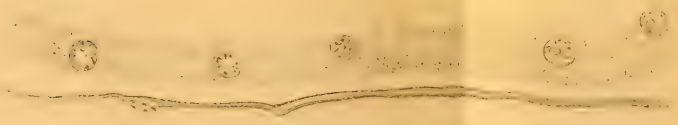


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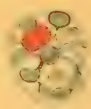
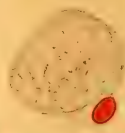
Fig 32^tFig 32^a

Fig. 32^c

Fig. 32^dFig. 32^e

Fig. 30.

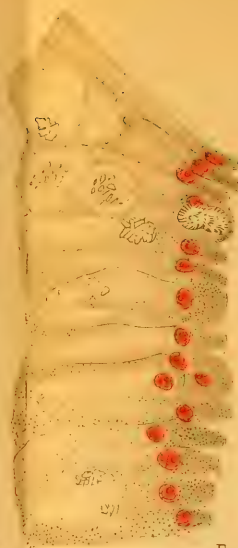


Fig. 27.



Fig. 28



Fig. 31.

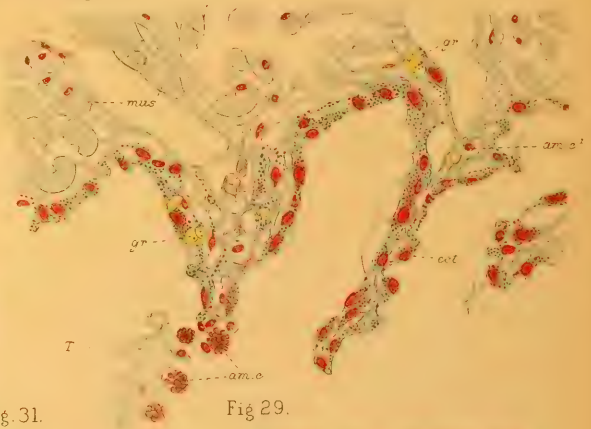


Fig 29.

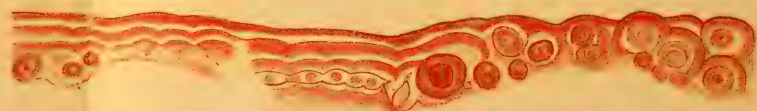
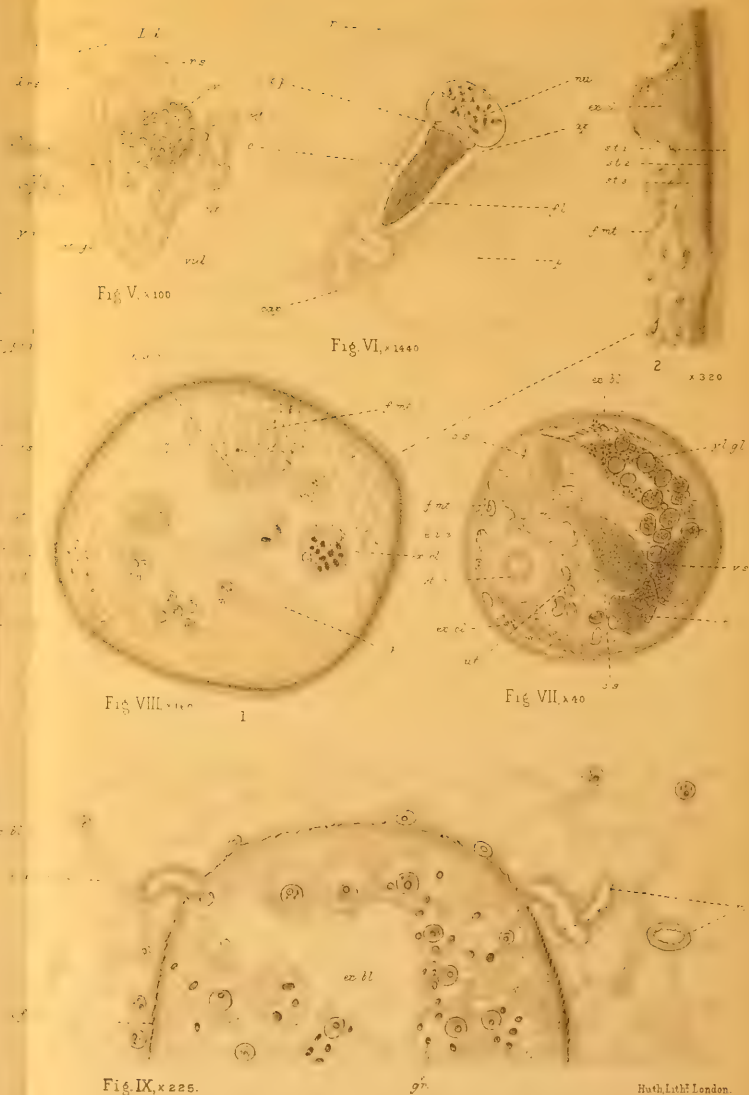
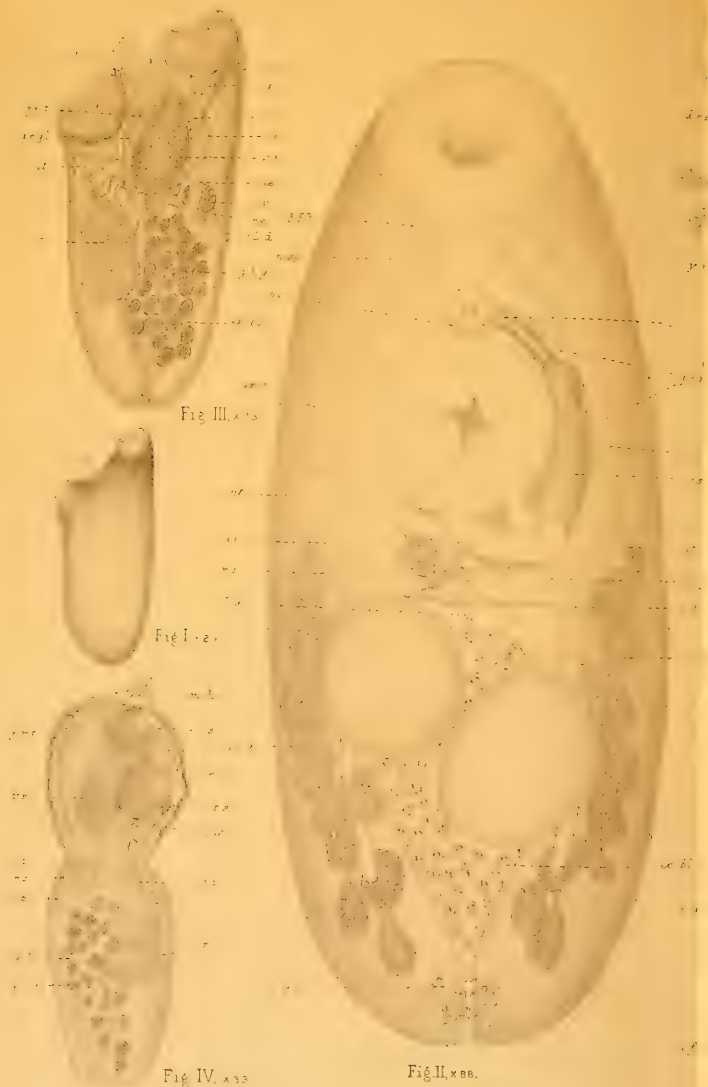
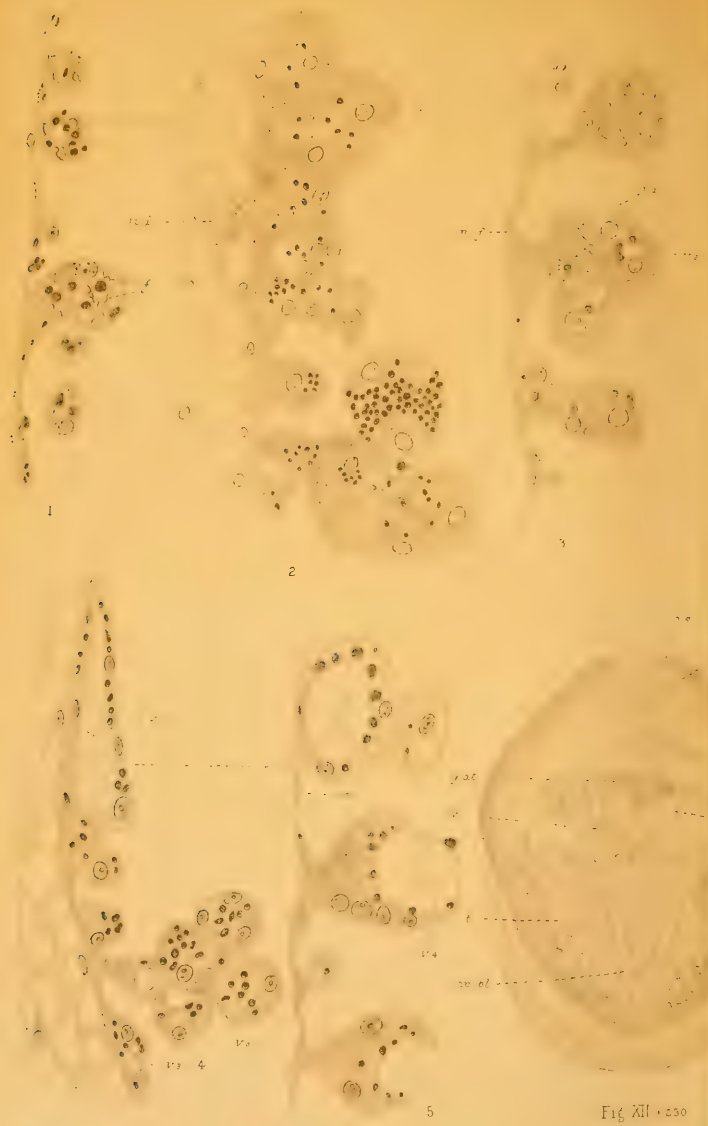


Fig 33.





Warren del



Warren del



Fig. XIII, x400.

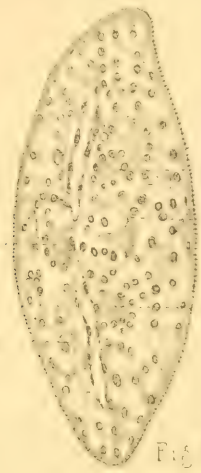


Fig. XVIII, x400.

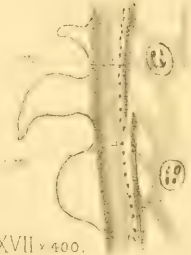


Fig. XVII, x400.

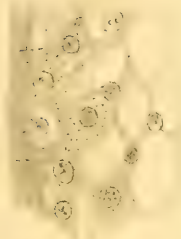


Fig. XIV, x400.



Fig. XV, x400.

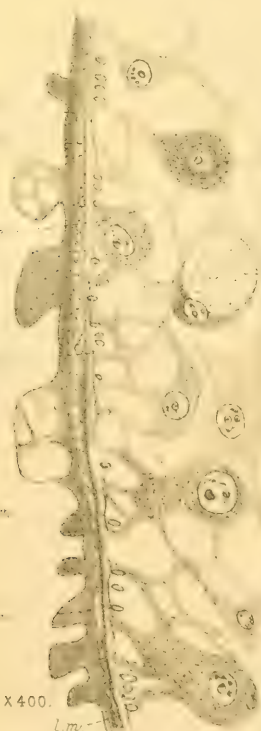


Fig. XVI, x400.





Fig. 1



Fig. 2.



Fig. 4.



Fig. 5



Fig. 6



Fig. 8.



Fig. 3.



Fig. 7.



Fig. 9



Fig. 10.



Fig. 11



Fig. 12

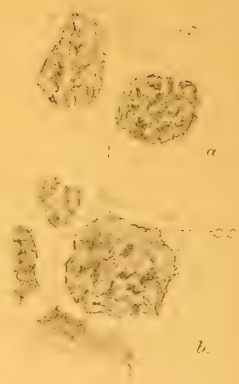


Fig. 13

Fig. 14

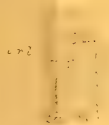


Fig. 15



Fig. 19

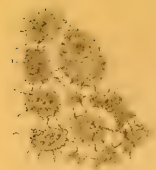


Fig. 16

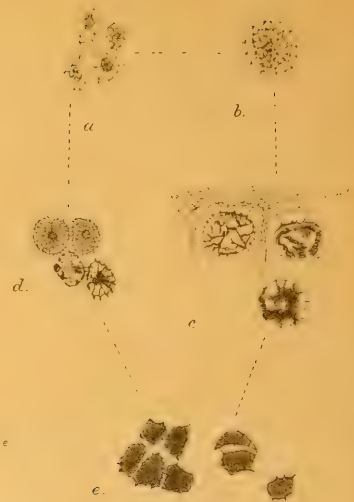


Fig. 17



Fig. 21

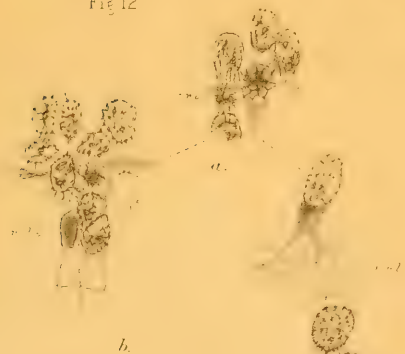


Fig. 18

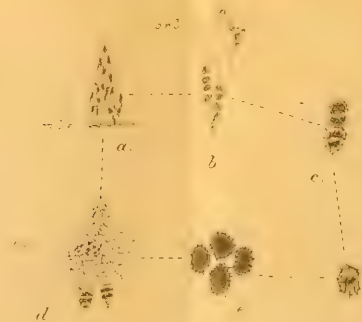


Fig. 20

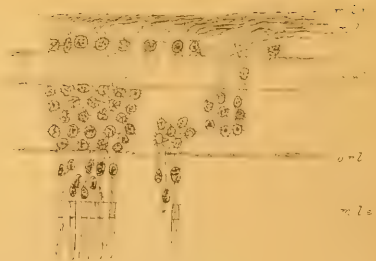


Fig. 22

H.M.B. delit.

Huth, Lith. London.

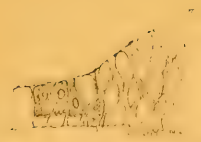


Fig 24



"

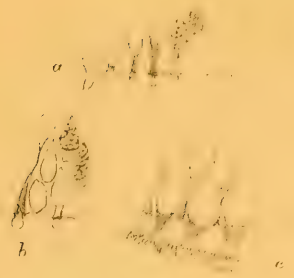


Fig 23



Fig 27.



Fig 25



Fig 28

"

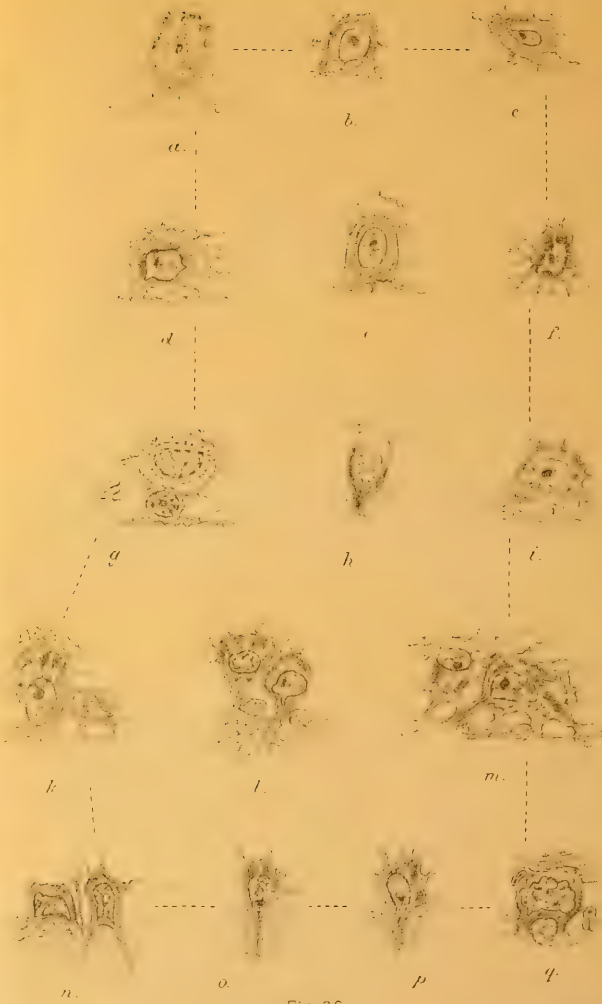


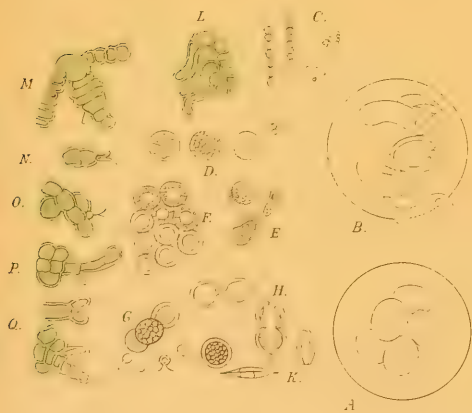
Fig 26



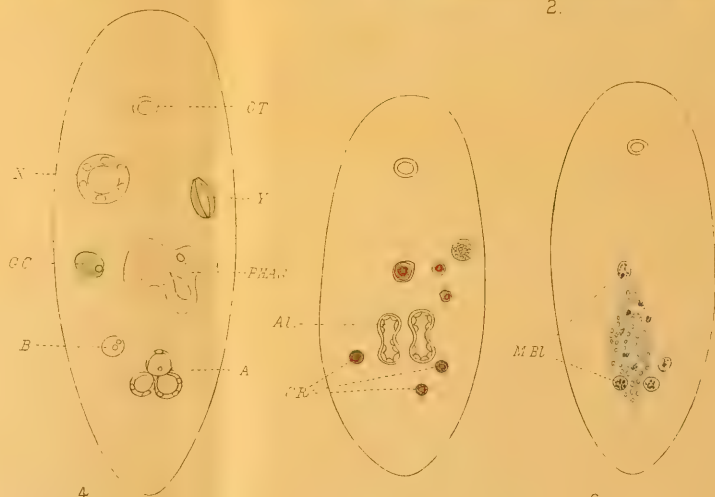
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2.



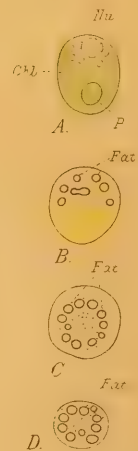
3.



4

5.

6.

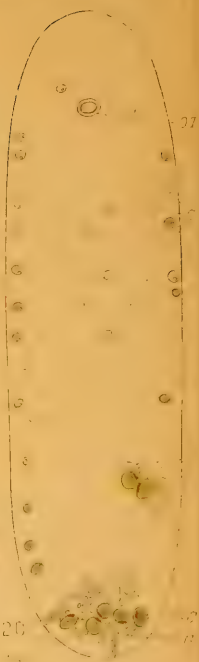
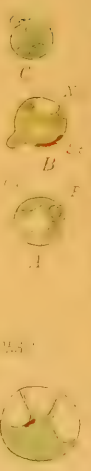
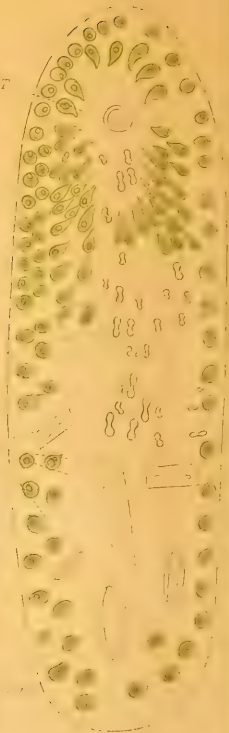


6^



10

11



20

27



18

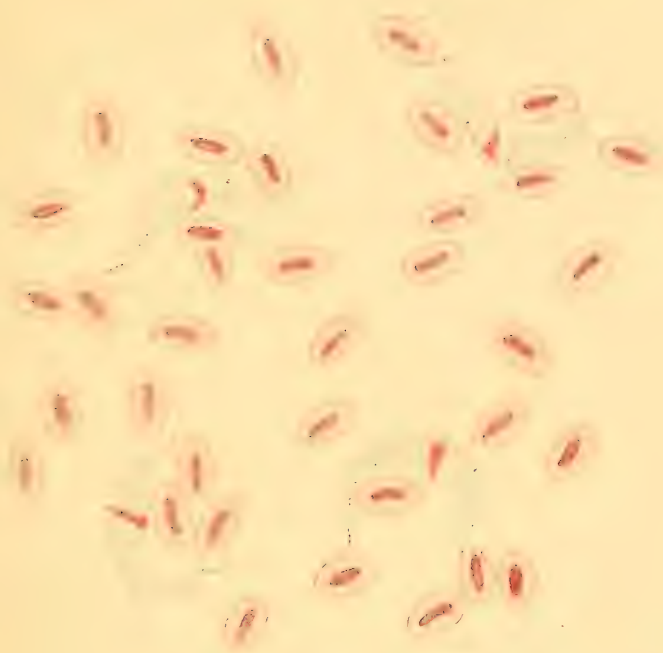


Fig. 1.
Trypanosoma of pigeon, (India).



Fig. 2.
Trypanosoma of crow, (India).

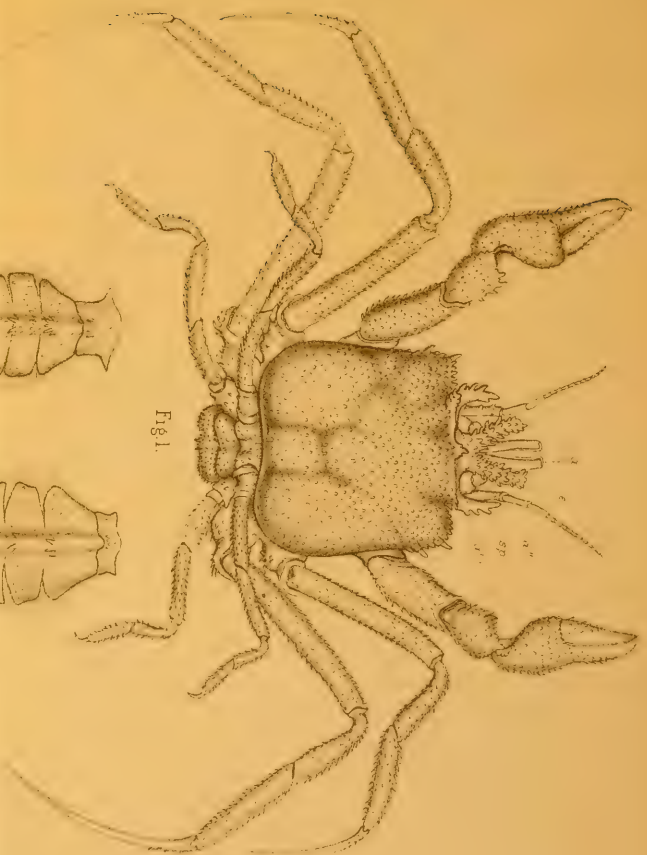


Fig. 1.



Fig. 3.

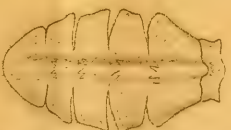


Fig. 4.



Fig. 5.



Fig. 6.

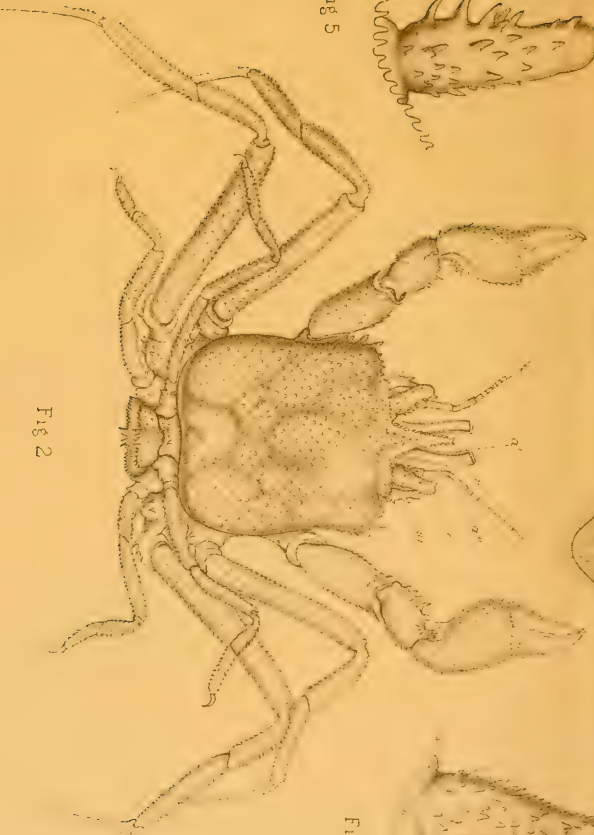


Fig. 2.



Fig. 7



Fig. 13.



Fig. 9.

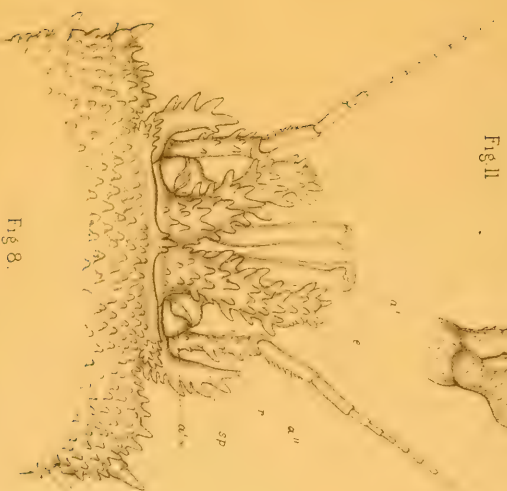


Fig. 8.



Fig. 12

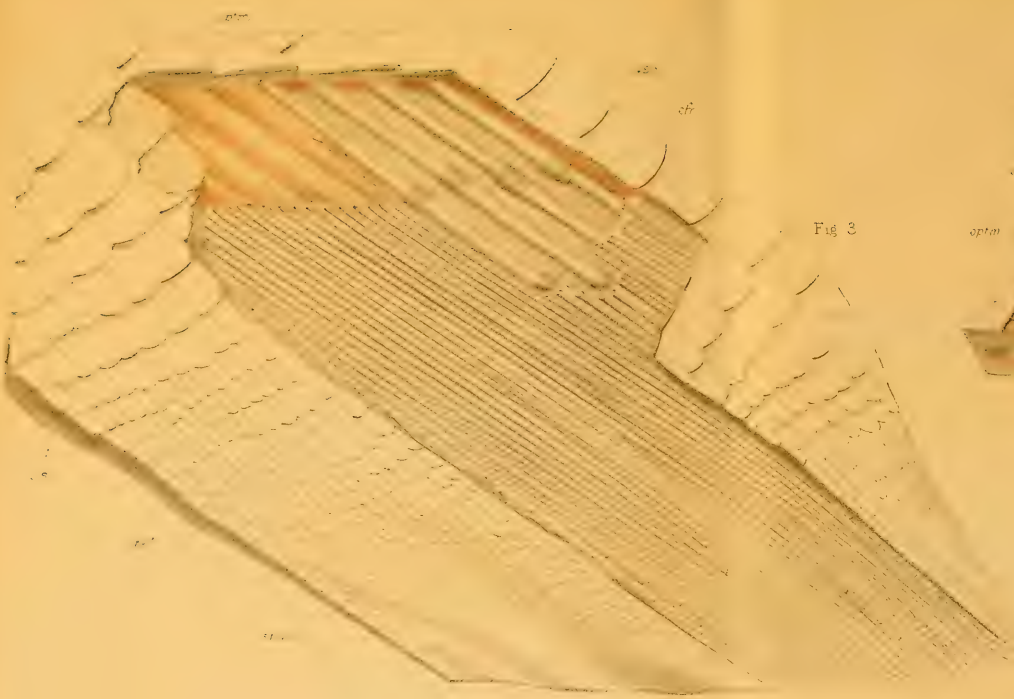


Fig. 3

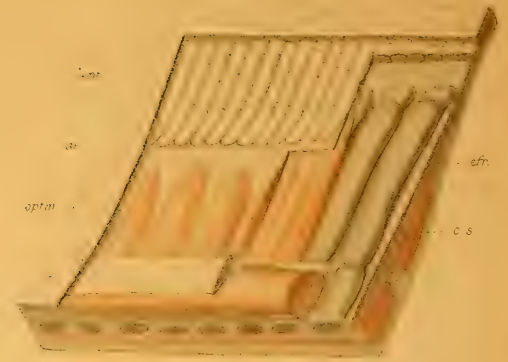


Fig. 2

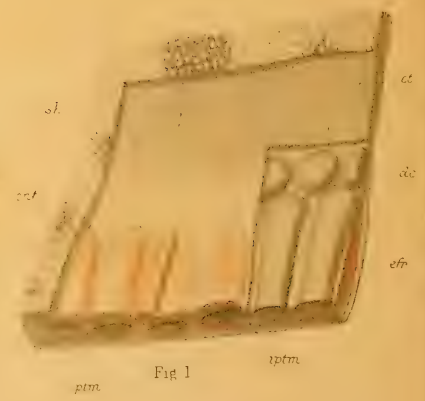


Fig. 1

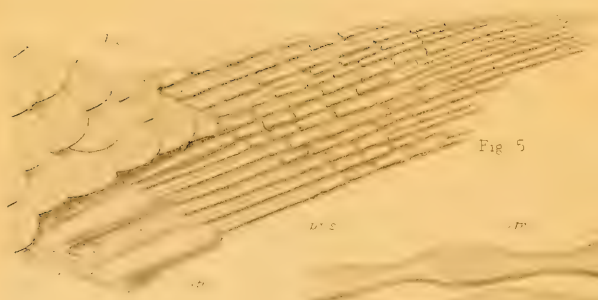


Fig. 5

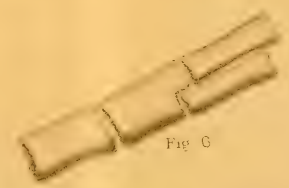


Fig. 6

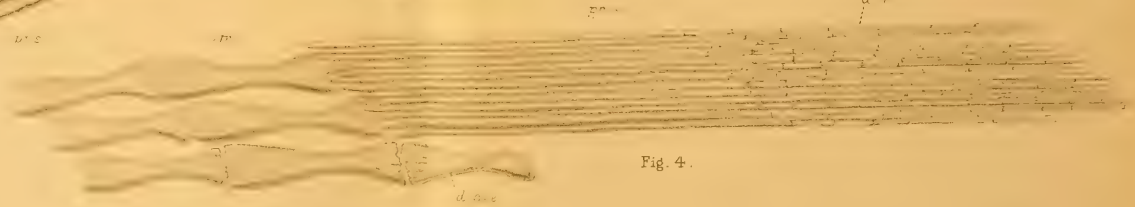


Fig. 4

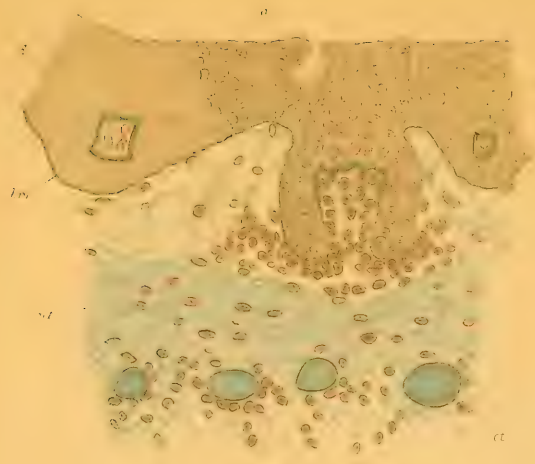


Fig. 9

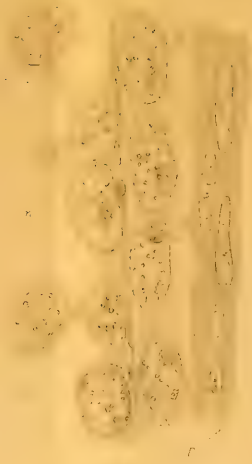


Fig. 8

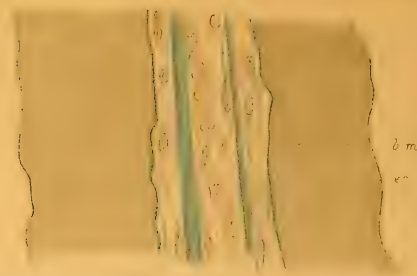


Fig. 7

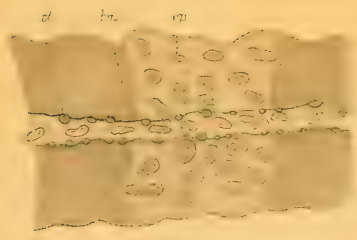


Fig. 10

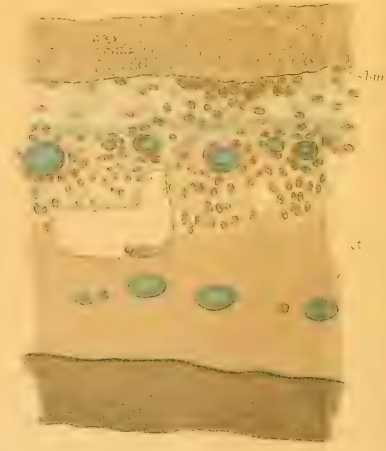


Fig. 11



Fig. 12

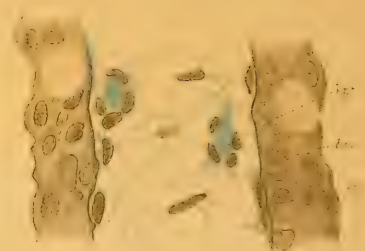


Fig. 13

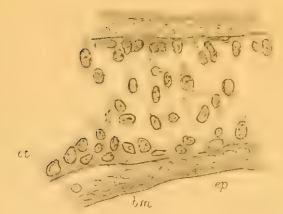


Fig. 12



Fig. 14

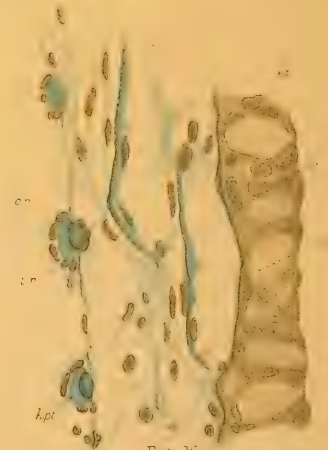


Fig. 16



Fig. 17



Fig. 18

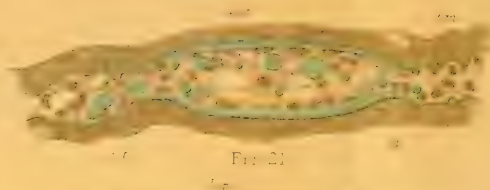


Fig. 19



Fig. 20

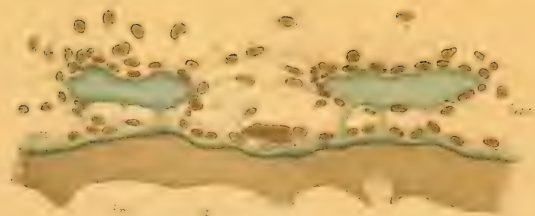


Fig. 21

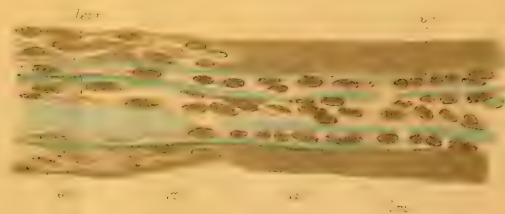


Fig. 22



Fig. 23



Fig. 24

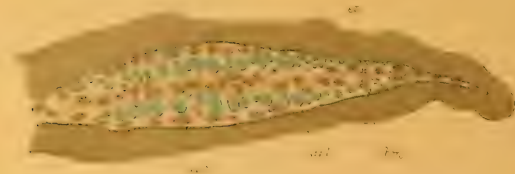


Fig. 25

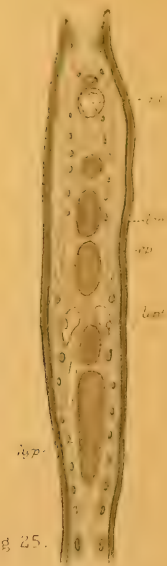


Fig. 26

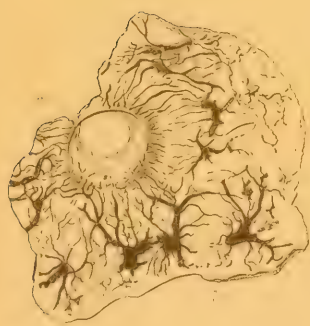
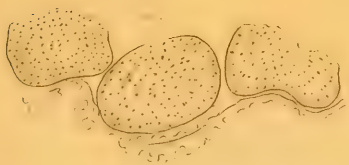
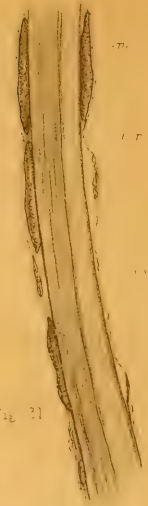
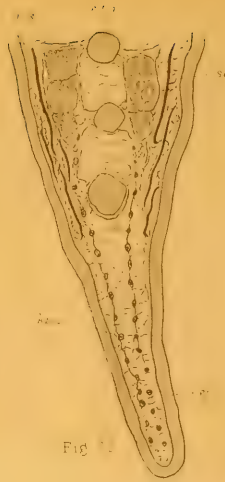
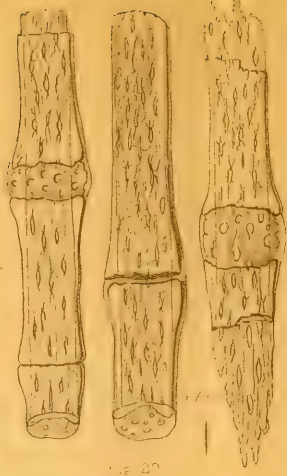
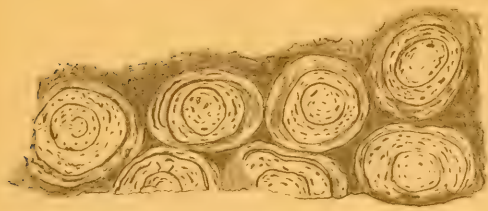




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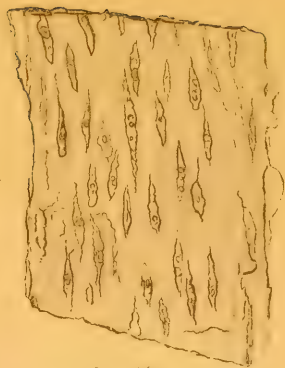


Fig. 41

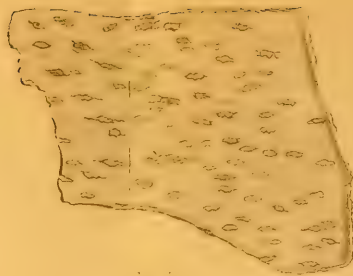


Fig. 42

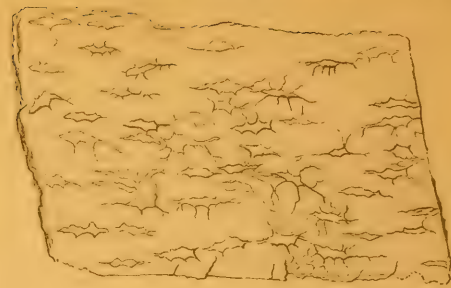


Fig. 43



Fig. 44

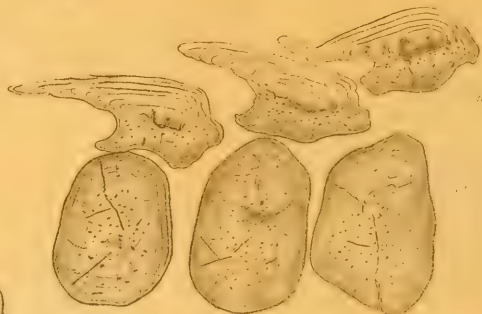


Fig. 45

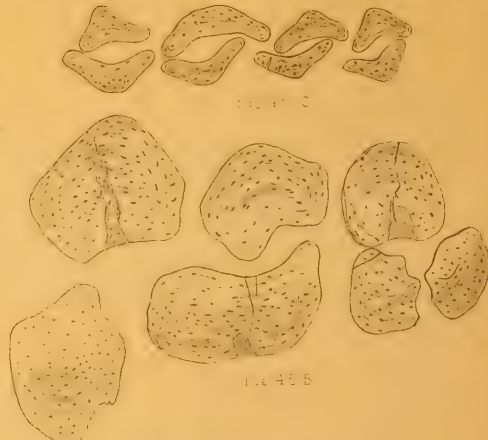


Fig. 46

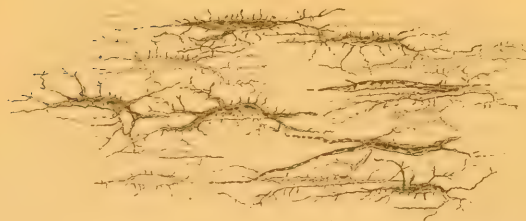


Fig. 47

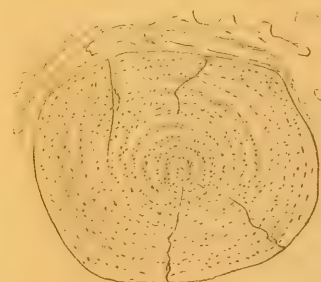


Fig. 48



Fig. 49

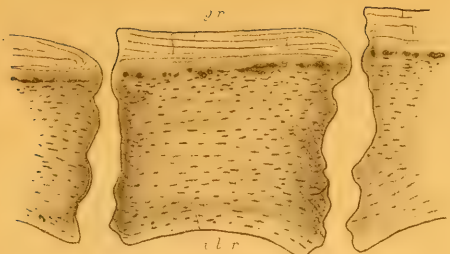


Fig. 48

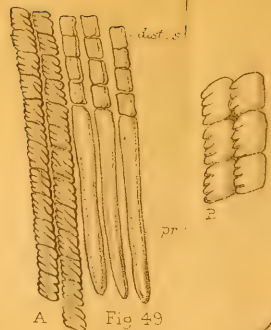


Fig. 49

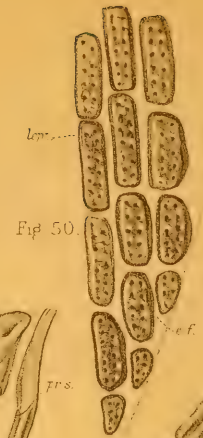


Fig. 50

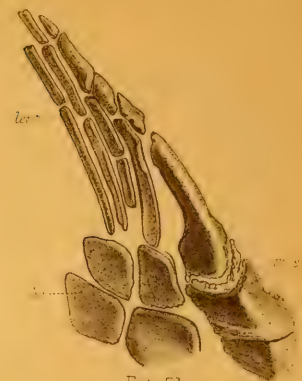


Fig. 51

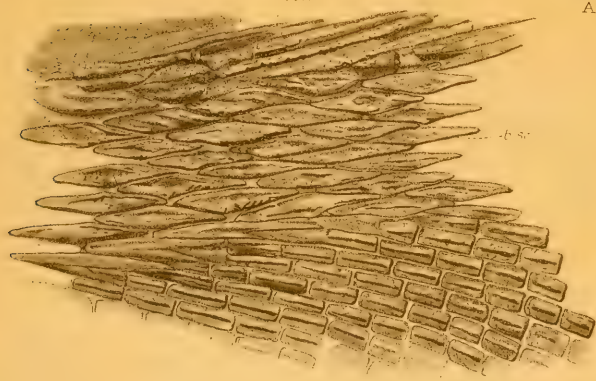


Fig. 52

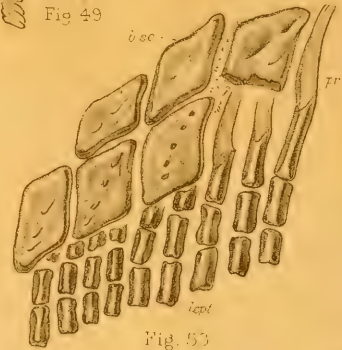


Fig. 53

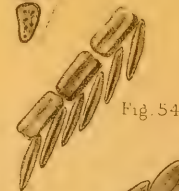
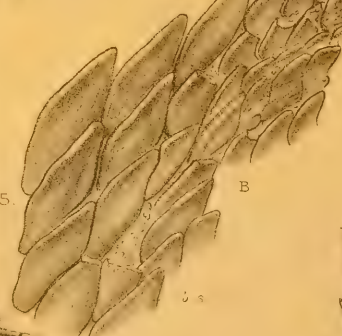


Fig. 54



Fig. 55



B



Fig. 57

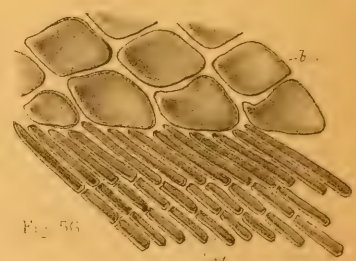
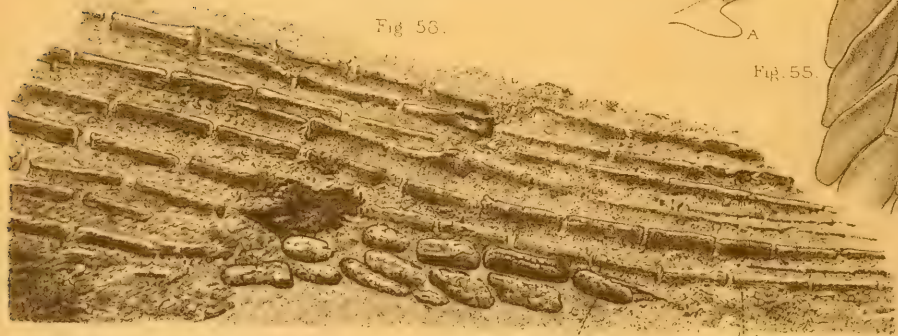


Fig. 56

Fig. 56



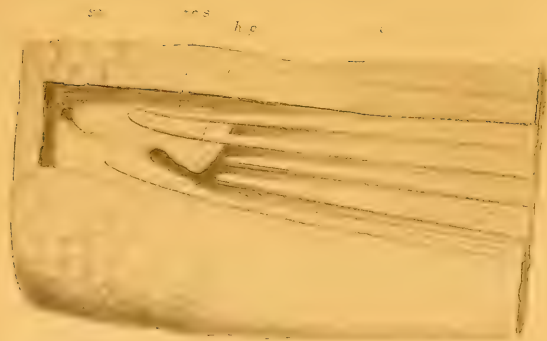


Fig. 59.



Fig. 60

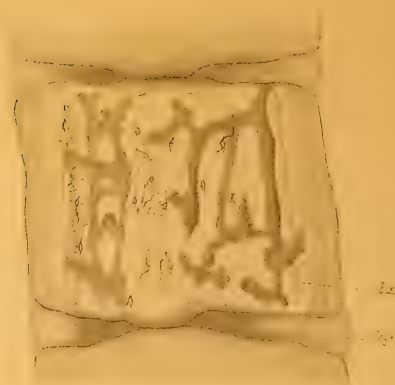


Fig. 61



Fig. 62.

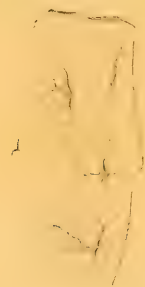


Fig. 63

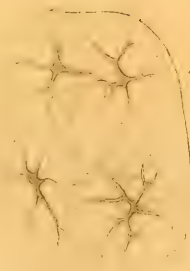


Fig. 64



Fig. 65

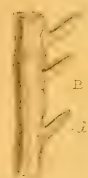
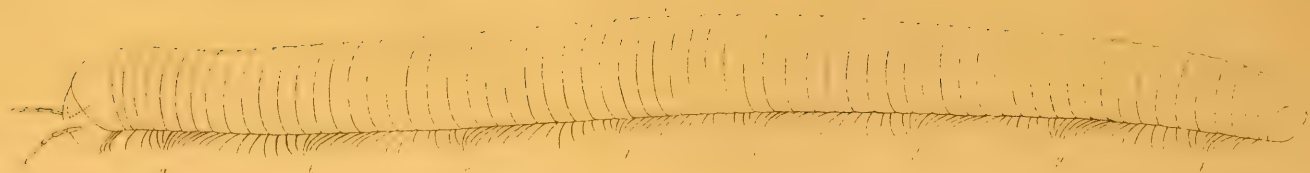


Fig. 66



Fig. 67





Archispirostreptus.

Fig 1

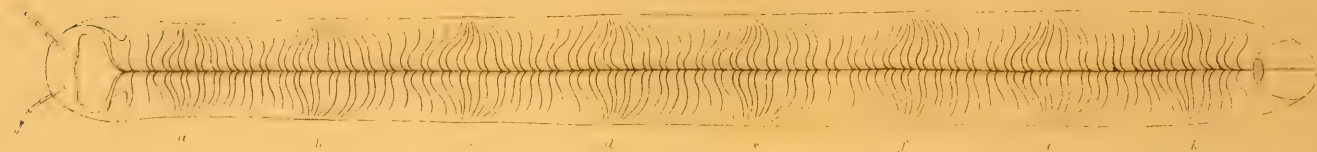


Fig 2.



Fig 3.

Scolopendra



Fig 8.



Fig 9



Fig 4

Peripatus



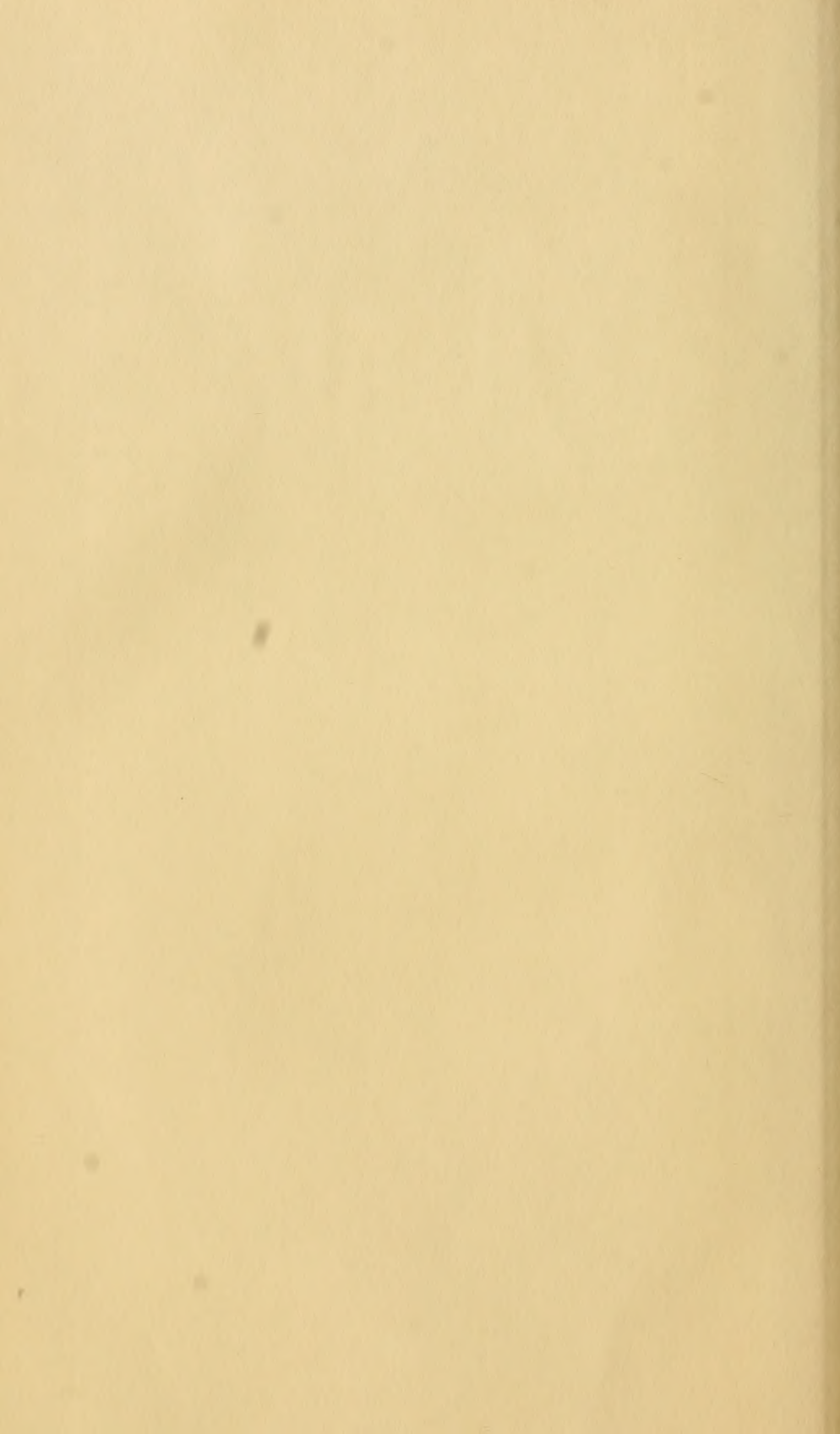
Fig 6



Fig 7



Fig 5.



3 2044 106 276 678

Date Due

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